

MANAGEMENT OF COREGONID FISHERIES: MULTIFORM AND MULTISPECIES PROBLEMS

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Academic dissertation in Fisheries Science

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Abstract

The polymorphism of the whitefish (*Coregonus lavaretus* (L.)) complicates fisheries management. In the same lake there are often several sympatric whitefish forms, with different growth rates and living habits. In many cases, some of these whitefish stocks reproduce naturally, while some are maintained by stocking. The density of the whitefish stock may vary greatly, especially in the pelagic stocks of small-sized fish. The growth of whitefish is generally density-dependent. Fluctuations in the vendace (*Coregonus albula* (L.)) stocks affect whitefish and the fishery. During periods of abundant vendace, the growth of whitefish may be reduced, and vice versa. The gill-net fishing of whitefish is a problem in the enhancement of salmonid predators such as brown trout (*Salmo trutta m. lacustris*). Many brown trout young that are still below the allowable catch size are taken as a by-catch in whitefish gill nets of small mesh sizes. This decreases the profitability of brown trout stocking and weakens the potential for recreational fishing on brown trout. On the other hand, large mesh sizes in gill-net fishing may lead to the underexploitation of whitefish, which in extreme cases causes dwarfing.

Single-species fish stock models have been used most commonly in research on whitefish fisheries management in Finland. However, more effective tools are needed to handle the multispecies effects of the fishery, interactions between fish species, and contradictions between different fisher groups.

Decision analysis was applied to the problems of a mixed fishery of whitefish and brown trout, and to study the effect of the restrictions on gill-net fishing on the predatory effect of brown trout on vendace during a low-density state. Bayesian influence diagrams were constructed to study the effect of restrictions on gill-net mesh sizes and effort on the benefit from whitefish and brown trout stocking, and indirectly on the spawning stock density and catches of vendace. It was found that it is possible to regulate the gill-net fishery so that stocking with both whitefish and brown trout is profitable, but the mesh size restrictions needed depend on the growth rate of whitefish, the significance of recreational fishing on brown trout, and the existence of commercial fishing on whitefish. The uncertainty and variability in the different factors affecting the stocking result is large, and therefore the effect of fisheries management may be difficult to detect in the short term. Adaptive management for the whitefish fishery is recommended. Whitefish is sensitive to disturbances in the environment or fish assemblage, and management should be able to adapt to the new situation. Different decision rules are needed for the low and high density states of vendace. This presumes a flexible fisheries management system.

Restrictions on whitefish fishing would not essentially affect vendace, the main prey species of brown trout, in spite of decreased mortality of brown trout. Dynamic modelling was used to examine the effects of predation on vendace in more detail. The results indicate that the role of perch (*Perca fluviatilis* (L.)) is more crucial than that of brown trout in maintaining recessions in vendace stocks. This study emphasizes the importance of dynamic modelling in studies on complex interactions between fish stocks, and on the effects of fishing and fisheries management.

Original articles and author's contribution

This thesis is based on the following original articles, referred to in the text by their Roman numerals:

- I. Heikinheimo-Schmid, O & Huusko, A. 1988. Management of coregonids in the heavily modified Lake Kemijärvi, northern Finland. *Finnish Fisheries Research* 9, p. 435–445.
- II. Heikinheimo-Schmid, O. 1992. Management of European whitefish (*Coregonus lavaretus* L. s.l.) stocks in Lake Paasivesi, eastern Finland. *Pol. Arch. Hydrobiol.* 39, p. 827–835.
- III. Raitaniemi, J. & Heikinheimo, O. 1998. Variability in age estimates of whitefish (*Coregonus lavaretus* (L.)) from two Baltic populations — differences between methods and between readers. *Nordic J. Freshw. Res.* 74, p. 101–109.
- IV. Heikinheimo, O., Miinalainen, M. & Peltonen, H. 2000. Diet, growth and competitive abilities of sympatric whitefish forms in a dense introduced population: results of a stocking experiment. *J. Fish Biol.* 57, p. 808–827.
- V. Heikinheimo, O. & Raitaniemi, J. 1998. Decision analysis as a tool in planning fisheries management — exemplified by the whitefish and brown trout fishery in Lake Lappajärvi, Finland. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* 50, p. 401–417.
- VI. Heikinheimo, O., Valkeajärvi, P. & Helminen, H. 2000. Interactions between brown trout, vendace, and the fishery in Lake Päijänne. *Arch. Hydrobiol. Spec. Issues Advanc. Limnol.* (Accepted).
- VII. Heikinheimo, O. Can predation maintain recessions in vendace stocks? A dynamic modelling approach. (Manuscript).

Author's contribution

- I. The article was based on the results of the fisheries subproject included in a large biological research project on Lake Kemijärvi. The author was the leader of the fisheries subproject. Ari Huusko was responsible for most of the data sampling, handling of the material and age determination of the fish. The author carried out the analysis of the whitefish data. The Finnish research report (Heikinheimo-Schmid & Huusko 1987a), on which the English article is based, was written jointly. The article published in English was written by the author.
- III. The study on whitefish age determination was planned jointly, and a some of the scales and bony structures used in age determination was delivered by the author. Jari Raitaniemi organised the test, analysed the results and wrote the article. The conclusions were written jointly.
- IV. The stocking experiment and data sampling was planned by the late Dr. Kalervo Salojärvi and carried out under his leadership. The stomach contents of whitefish were analysed and the food consumption estimated by Matti Miinalainen, guided by the author. Heikki Peltonen was responsible for the analysis of growth and population size. The article was written jointly.
- V. The author planned and carried out the decision analysis and wrote the article. The data on which the parameter values were based was sampled and mainly analysed by Jari Raitaniemi.
- VI. The author was responsible for the idea and the modelling analysis, and wrote the greater part of the article. The parameter values used were partly based on unpublished research results or data by Pentti Valkeajärvi and Harri Helminen.

1. Introduction

The coregonids whitefish (*Coregonus lavaretus* (L.)) and vendace (*Coregonus albula* (L.)) belong to the economically most important fish species in Finland. Substantial private and public funds are used on the stocking of whitefish. Vendace is the dominant pelagic planktivore fish species, and the most important target species of commercial fishing in Finnish inland waters. Generally, coregonids are highly adaptable to diverse environmental conditions and are widely distributed throughout the Holarctic (Luczynski 1995). They support substantial commercial, subsistence, and recreational fisheries.

The polymorphism of the whitefish complicates fisheries management (Lindsey 1988). In the same lake there are often several sympatric whitefish forms, with different growth rates and living habits (Svårdson 1979). In many cases, some of these whitefish stocks reproduce naturally, and some are maintained by stocking. Some of these stocks are endangered (Kaukoranta et al. 1998). The density of the whitefish stock may vary greatly, especially in pelagic stocks of small-sized fish. The growth of whitefish is generally density-dependent (Salojärvi 1992a).

Large variations in year-class strength are typical of vendace stocks (Viljanen 1986), and during the past 20 years, there have been prolonged periods of low density in the vendace stocks in several lakes (Valkeajärvi et al. 2000). The unpredictability of future vendace yields poses severe problems in commercial fishing in inland waters (Sipponen et al. 1999). Moreover, the density of vendace affects whitefish and the fishery of the species. During periods of abundant vendace, the growth of whitefish may be reduced, and vice versa (Raitaniemi et al. 1999).

A unique feature of the fishery in Finland is the prevalence of gill-net fishing. In addition to most of the commercial catch (Kalatalous ajassa 1993), more than 90% of the whitefish catch of recreational and subsistence fishermen is taken with gill nets (Recreational fishing 1994, 1996, 1998). Therefore, the problems in fisheries management in Finland are somewhat different from those in other parts of Europe (e.g. Cowx 1998), or in North America, where gill nets are usually not allowed for recreational fishing.

By-catches are generally abundant in the Finnish gill-net fisheries. In the gill-net fishing for whitefish, young predator fish such as brown trout (*Salmo trutta m. lacustris*) are commonly entangled (Makkonen et al. 1996). A great deal of the stocked brown trout are caught with gill nets during their first year in the lake. This leads to poor stocking success with brown trout and decreases the value of recreational fishing. Furthermore, this causes controversies between commercial and recreational fisheries, or gill-net and rod fishermen (Makkonen et al. 1996, Heikinheimo & Valkeajärvi 1998). On the other hand, use of large mesh sizes in gill-net fishing may lead to underexploitation of small-sized whitefish (Table 1), which in extreme cases may cause the dwarfing of the whitefish (Salonen & Mutenia 1992, Amundsen et al. 2000).

Similar problems arise in cases where the protection of threatened fish species or stocks, mostly salmonid predators, is one target of fisheries management (Salmi et al. 2000). In Finland, the greatest threat to the survival of these stocks, besides the degradation of reproduction areas, is gill-net fishing.

Debate has been raised in Finland about the possible role of brown trout stocking in the fluctuations of the vendace stocks, and recommen-

Table 1. A schematic presentation of the expected interactions between gill-net fishing, whitefish (slow growth/rapid growth) (W), brown trout (B) and vendace (V). Symbols (+, –) indicate the positive or negative direction of the effect.

Gill-net fishing	Exploitation of whitefish	Stocking result		Stock density			Growth rate		
		W	B	W	B	V	W	B	V
Small mesh size	Effective/overfishing	+/-	–	–	–	+	+	+	–
Large mesh size	Ineffective/suitable	–/+	+	+	+	–	–/+	–	+

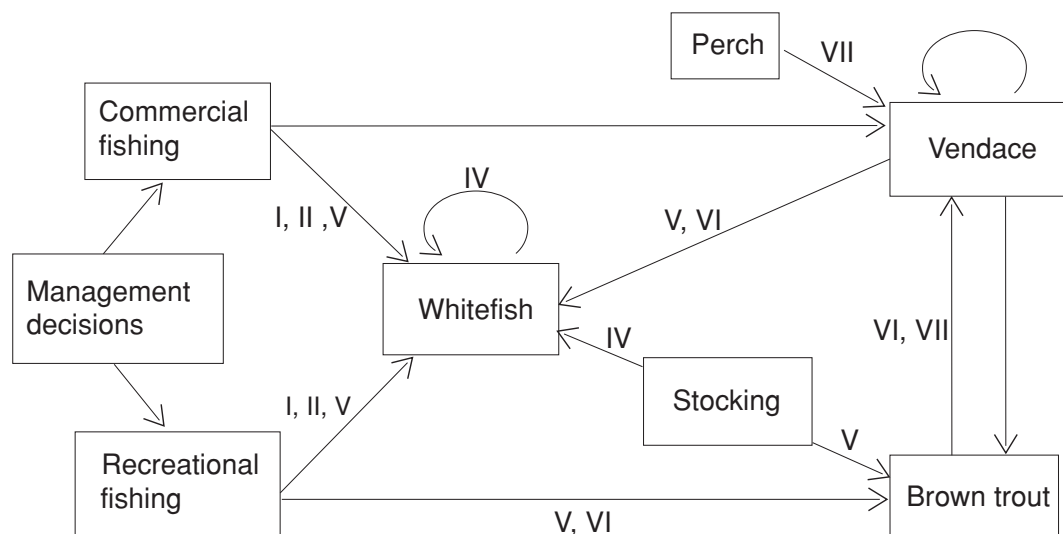


Fig. 1. The main interactions in the coregonid fishery system. The Roman numerals refer to the original articles where the specific causalities were examined.

dations have already been given to restrict brown trout stocking in vendace lakes (Helminen & Sarvala 1994, Marttunen & Kymälä 1997, Vehanen et al. 1998). This has most probably been one reason that the number of brown trout stocked decreased by half from 1996–1998 (Fish and crayfish stocking statistics 1998). On the other hand, assumptions have been presented that perch, as a predator of young-of-the-year vendace, may play a role in the dynamics of vendace stocks, because a high abundance of perch has been observed in the pelagic zone during periods of low vendace density (Auvinen 1994, Helminen & Sarvala 1994, Valkeajärvi & Bagge 1995).

There has been discussion on the indirect effect of gill-net fisheries management on vendace as well (Vehanen et al. 1998). The restriction of whitefish gill-net fishing would decrease the mortality of brown trout during the first year after stocking (Heikinheimo & Valkeajärvi 1998). Accordingly, if more brown trout avoided the gill nets, the predation pressure on vendace could increase (Table 1).

2. Aims of the study

This thesis is focused mainly on the management of the whitefish fishery in inland waters and the effects of the management on other fish species

and their interactions (Fig. 1). Management of the vendace fishery is not examined directly. Vendace is dealt with as a species that has a significant impact on whitefish and its fishery, and that, on the other hand, may be indirectly influenced by the whitefish fisheries management. Moreover, vendace was used as an object for examining the suitability of dynamic modelling in studying the complex interactions within the fish assemblage (VII). The dependency of the growth of brown trout on the density of vendace (Table 1, Fig. 1, Niva 1999) is not examined but is taken into account in the model in the article VI.

The following core issues are examined in this thesis:

- 1) Management of the fishing of different whitefish forms to ensure sustainable exploitation and effectivity of stocking (I, II, IV, V).
- 2) Implementation and relevance of management advice given to the whitefish fishery in the 1980s (I, II).
- 3) Management of the mixed fishing of whitefish and brown trout (V).
- 4) Indirect effects of whitefish fisheries management on interactions in the fish assemblage: predation on vendace (VI, VII).
- 5) Usability of the modelling methods, and sources of uncertainty in the research on the management of coregonid fisheries (III, VI, VII).

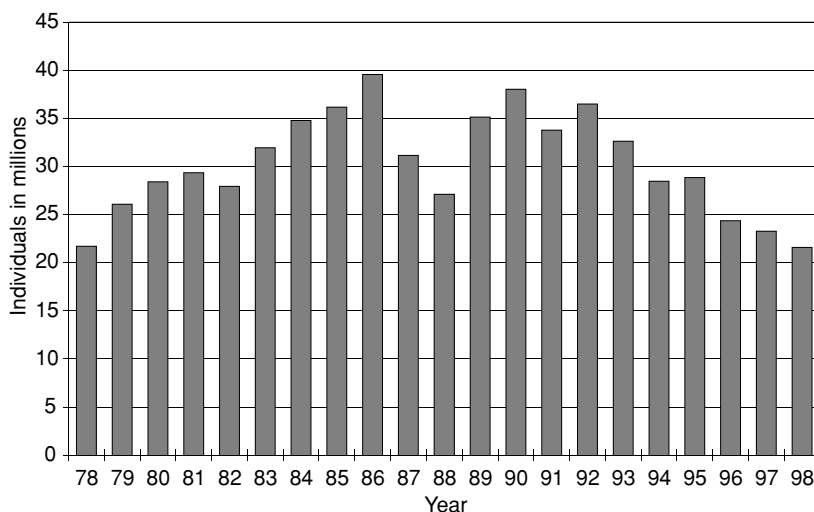


Fig. 2. Numbers of whitefish juveniles raised in natural food ponds for stocking purposes in Finland in 1978–1998. Newly hatched fry are not included (Regional fisheries in Finland 1999).

3. Background

3.1. Fishing and stocking of coregonids in Finland

Whitefish is one of the fish species most commonly used in stocking in Finland (Fig. 2). The purpose of stocking is to enhance the commercial and recreational fishery, or in many cases to compensate for losses caused by habitat modification. In 1998, more than 20 million one-summer-old or older, and about 70 million newly-hatched larvae were stocked (Fish and crayfish stocking statistics 1998). About half of the newly-hatched and 60% of the older whitefish young were released into inland waters (R. Savolainen, Finnish Game and Fisheries Research Institute, personal communication).

In inland waters, the annual whitefish catch from the commercial fishery has varied from 200 tonnes to 800 tonnes in the 1980s and 1990s (Fig. 2). Most of this was taken from the province of Lapland. The average annual commercial whitefish catch from the Finnish sea area, during the same period, has been about 1000 tonnes. In the 1980s, the value of the whitefish catch was about 10% of that of the total commercial catch from inland waters. Besides whitefish stocking, the abundance of vendace affects the whitefish catches. The catch from inland waters increased at the beginning of the 1990s, when vendace stocks were sparse in many lakes (Fig. 3), and whitefish of-

fered a substitute for vendace in the commercial fishery of inland waters. During this period of low vendace catches, the relative value of whitefish in the total catch increased to 17% in 1998 (Commercial inland fishery 1998). During the latter half of the 1990s, there seemed to be a decreasing trend both in the amount of whitefish stocked and in the catches, but an upward trend in the vendace catches (Figs. 2 and 3).

The whitefish catch of recreational and subsistence fishermen from the inland and sea area was in total 4000–6000 tonnes from 1984–1992 (Kalatalous ajassa 1993), 4400 tonnes in 1994, and 3000–3400 tonnes from 1996–1998, two thirds of which was taken from lakes (Recreational fishing 1994, 1996, 1998). The share of the recreational and subsistence fishery of the total whitefish catch from inland waters was 83% in 1998 (Recreational fishing 1998).

The results of whitefish stocking have been variable. According to Salojärvi (1992a), the catch from stocking with one-summer-old fingerlings in northern Finland has been from 2–250 kg (from 55–60 kg on the average) per 1000 stocked fingerlings. In many cases, the success of stocking has been poor because fishing has failed to exploit the whitefish effectively, or the stocking density has not been correctly determined in relation to the fishing effort (Salojärvi 1992a). This has in some cases led to the dwarfing of the whitefish because of the overdensity of the stock (Sarjamo et al. 1989).

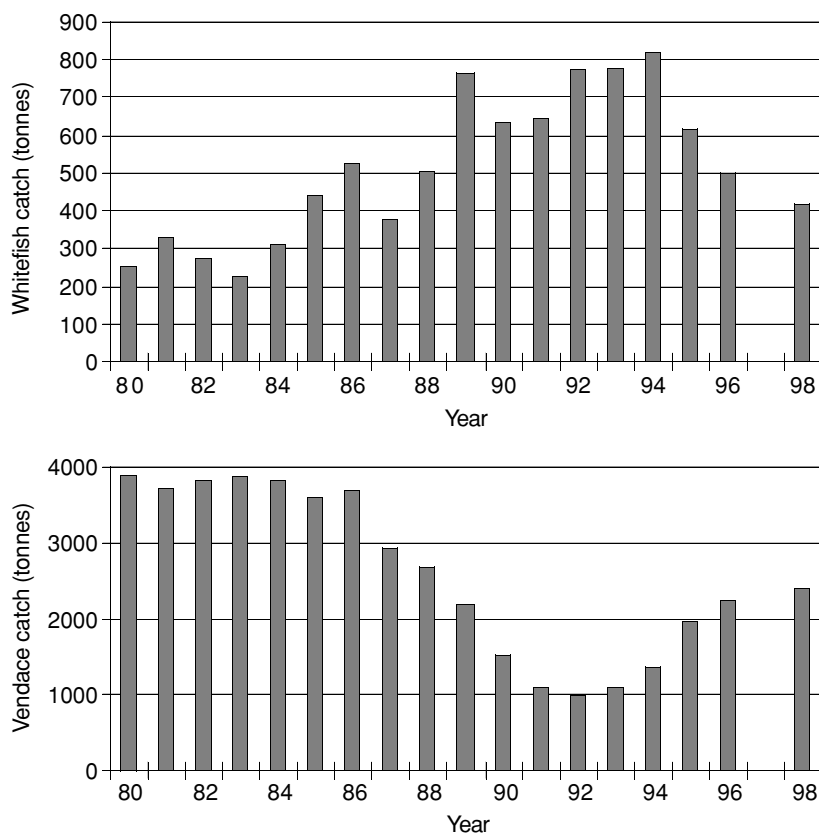


Fig. 3. The whitefish and vendace catches of commercial fishing in Finnish inland waters from 1980–1996 (Kalatalous ajassa 1993, Commercial inland fishery 1992, 1993, 1994, 1995, 1996, 1998). Catches were not registered in 1997.

3.2. The whitefish forms in Finland

Whitefish is distributed throughout northern Europe, in both fresh and brackish waters. Wide variation in ecology, life history and morphology is typical of this species. According to the current understanding of whitefish taxonomy, there is only one native whitefish species, *Coregonus lavaretus* (L.) in Finland but there are several forms which differ in their morphology and biology (Himberg & Lehtonen 1995). Another whitefish species used for stocking in some Finnish lakes, peled whitefish (*C. peled*), has been imported from Siberia.

Typically, two or more whitefish forms live sympatrically in the same lake. Svärdsön (1979) named six different forms of *C. lavaretus*, most of which can be separated on the basis of their gill-raker density. Some forms have the same gill-raker density but different living habits and spawning areas (Table 2). This classification is currently generally applied in Finland, although it cannot

explain all cases, and there may be intermediate forms (Kaukoranta et al. 1998). Three-part scientific names are recommended for the whitefish forms (Himberg & Lehtonen 1995), for instance *Coregonus lavaretus pallasii*, known as “plankton whitefish” in Finland, or “northern densely-rakered whitefish” by Svärdsön (1979). The whitefish forms do not fill the criteria of subspecies in all relations, but this kind of nomenclature is used in the text, because it is considered to be sufficiently clear and accurate for the purposes of fisheries management. The earlier practice, presented by Svärdsön (1979), was to use species names for the whitefish forms, such as *Coregonus pallasii*. This nomenclature was used in the articles I and II.

Among whitefish, the river-spawning *C. l. pallasii* stocks have been classified as severely endangered (Kalaston suojelutyöryhmän muistio 1996, Kaukoranta et al. 1998). The general situation of the other whitefish forms is not thoroughly

known, but many naturally reproducing populations have declined, or only a few of them exist. The lake-spawning *C. l. nilssonii* was not classified as endangered by the Working Group on the Protection of the Fish Community in 1996 (Kalaston suojelutyöryhmän muistio 1996), but according to Kaukoranta et al. (1998), there are only a few self-sustaining stocks left. The reproduction of lake-spawning whitefish stocks is disturbed by the water-level regulation in many lakes, such as Lake Kemijärvi (I) and Lake Lappajärvi (V, Raitaniemi et al. 1995). The obscurity of the whitefish systematics complicates the outlining of the needs of protection. Original whitefish stocks may have been destroyed or weakened due to their mixing as a consequence of introductions (Kallio-Nyberg & Koljonen 1988, Kaukoranta ym. 1998).

3.3. Decision-making organisations in Finnish inland fisheries

Fisheries management in Finland is regulated partly by the Fisheries Act, and locally by Fishery Districts, fishery regions and statutory fishery associations. In addition, there are advisory organisations.

The statutory fishery associations are made up

of all the property owners in a village who have a share in the common water areas of that village. They manage about 90% of the inland water area (Sipponen 1995). Public fishing rights are provided for the public water areas in a few of the largest lakes, such as Lake Paasivesi (I).

In 1983, Finland was divided into 11 provincial Fishery Districts, subordinated to the Ministry of Agriculture and Forestry, and consisting of 222 fishery regions. Since 1997, these are incorporated into Employment and Economic Development Centres. They play a central role in implementing the Fisheries Act at the regional level (Sipponen et al. 1999).

The fishery regions were founded in order to promote planning and decision-making in fisheries for larger water areas (Salmi & Auvinen 1998). They are organs for co-operation uniting all those engaged in fishing and fisheries. The membership of a fishery region consists of statutory fishery associations, individual owners of waters, associations of professional and recreational fishermen, and in some cases, the Finnish state. The tasks of a fishery region include, for instance, preparing a management plan for its waters, collecting data on fishing, drawing up regulations governing fishing practices and supervising fishing (Sipponen et al. 1999).

Table 2. The whitefish (*C. lavaretus*) forms existing in Finland and their current distribution according to Kaukoranta et al. (1998). The classification is based on Svärdson (1979).

Name of the whitefish form	Average number of gill rakers	Spawning areas	Distribution in Finland
<i>C. l. fera</i>	18–22	Rivers and shallows in lakes	A few northern lakes (e.g. L. Inari)
<i>C. l. widgrenii</i>	25–31 in the sea area 23–24 in lakes	Shallows in the sea or in lakes	Coastal waters of the Baltic A few eastern and northern lakes
<i>C. l. lavaretus</i>	27–31	Rivers	Sea area and in rivers flowing into the Baltic; the Oulujoki and Vuoksi water systems
<i>C. l. wartmanni</i>	29–37	Lakes	Inland waters throughout the country
<i>C. l. nilssonii</i>	40–45	Lakes	Inland waters in southern and central Finland
<i>C. l. pallasi</i>	50–56	Rivers	Inland waters in central and northern Finland

3.4. The goals of fisheries management in Finland

The Finnish Fisheries Act from 1982 (1§) specifies the goal of fisheries management as to obtain the maximum sustainable productivity of fishing waters. Hence, the current Fisheries Act is based on utilization, whereas the previous one was based on the conservation of fish stocks (Sipponen 1995). However, restrictions on fishing have remained the most common means by which fisheries legislation supports fisheries management (Sipponen 1995).

A common concept in international fisheries management has been the maximum sustainable yield (MSY), which means maximizing the catch within the limits set by the endurance of the fish stock (Hilborn & Walters 1992, Charles 1994, Francis & Shotton 1997).

A more modern concept is called “optimum yield”, which recognises that cultural, social, political, economic and biological goals must be addressed (Barber & Taylor 1990).

There are no generally applicable and exactly defined goals and objectives for the management of different types of fisheries in Finland.

The goal of maximum sustainable productivity is most applicable for commercial fisheries. In addition, a constant supply of fish is important. The management should then maintain a broad age composition in the exploited stock. The fluctuation in the catches is less accentuated when the catch consists of several age groups, because occasional weak year classes do then not cause any significant drop in the catch.

Subsistence fishing, often considered a subtype of recreational fishing, can be defined as fishing for personal consumption, food for others, or for sale to supplement income (Cowx 1998). Most of the gill-net fishing in Finnish inland waters belongs to this type of fishery. The goals of subsistence fishing are partly the same as those of commercial fishing as the regularity of the supply is important. The diversity of the fish assemblage is an advantage, because recreational aspects are involved in subsistence fishing as well.

The general aim of recreational fisheries management in Finland has been to enhance large-sized predatory fish species. The option to catch

large fish can maintain the fishery even if the catches were rare. In this respect the gill-net fishing of whitefish is a problem, because it tends to take young predatory fishes and decrease their proportion in the fish assemblage.

General objectives of fisheries management also include profitability of stocking, protection of threatened species or stocks, and maintenance of versatile possibilities for fishing. With the recreational fishery, the concept of economical profitability may be debated (e.g. Sipponen 1999). There is no agreement on how the value of recreational fishing should be measured, but expenditure on it is high (Cowx 1998). The goals of fisheries management depend then on the environmental circumstances of the area, the type of fishery exercised and supported, and the species on which the fishing is targeted.

4. Material and methods

4.1. Study lakes

Lake Kemijärvi (I) is the northernmost of the study lakes (Fig. 4). Lakes Paasivesi (II) and Vuokalanjärvi (IV) are situated in eastern Finland and belong to the Saimaa lake system. Lake Lappajärvi (V) is the largest crater lake in Finland, situated in the western part of the country. Lake Päijänne (VI, VII), southern Finland, is the second largest lake in Finland. Lakes Kemijärvi, Lappajärvi and Päijänne are regulated for water power purposes and loaded by waste waters. The effects of habitat modification are strongest in Lake Kemijärvi (I), while Lakes Paasivesi and Vuokalanjärvi are least affected (II).

Different whitefish forms, both native and introduced, and vendace and brown trout are present in all the lakes studied (Table 3). In some cases the whitefish form cannot be named exactly, or the native forms may be affected by the stocked whitefish, resulting in intermediate forms. Vendace show fluctuations in all lakes, and brown trout is stocked. The role of these species was studied in Lakes Lappajärvi and Päijänne (V, VI, VII).

The cases studied represent widely typical Finnish coregonid lakes and management problems in different parts of the country. *C. l.*

wartmanni is the most abundant native whitefish form with a wide distribution, and *C. l. pallasii* is the form most commonly used for stocking. Different types of fishing are present in all the lakes studied, and lakes affected by habitat modification are included. An exceptional coregonid lake in Finland, not studied here, is the highly productive and effectively exploited Lake Pyhäjärvi in south-western Finland, where both whitefish and vendace originate from introductions (Sarvala et al. 1998). One example of an extremely complex coregonid assemblage is Lake Inari in northern Finland. There are four original whitefish stocks, two of which are dwarf whitefish, in addition to the introduced coregonids, *C. l. pallasii* and vendace (Mutenia & Salonen 1991). However, the basic management problems are similar in these lakes too, and in the coastal waters of Finland, despite different coregonid stocks.

In Lake Kemijärvi (I, Fig. 4) whitefish and brown trout have been stocked as compensation for the losses caused to the fishery by habitat modification. The reproduction of the original whitefish stocks was hindered because of water-level regulation. The fish stocks and fisheries in Lake Kemijärvi were studied in connection with an extensive project, which included studies on water quality, plankton, bottom fauna and littoral vegetation (Nenonen 1987). The purpose of the project was to provide information on the state of the lake and on the influence of human activities, and to make proposals for further development of the fisheries and monitoring of the lake ecosystem.

The second case is Lake Paasivesi (II, Fig. 4), part of the Vuoksi lake system, where a naturally reproducing, lake-spawning whitefish stock and stocked densely-rakered whitefish were fished simultaneously. The main purpose of the stocking was that *C. l. pallasii* could offer an alternative target species for commercial fishermen during low-density periods of vendace.

In Lake Vuokalanjärvi (IV), an experimental whitefish stocking was carried out to examine the possible differences between the whitefish forms and stocks in an overdense population. In Lakes Lappajärvi (V) and Päijänne (VI, VII), the whitefish and brown trout stocking is based mainly on compensatory obligations settled by courts.



Fig. 4. The location of the study lakes.

4.2. Single-species models

Single-species population and yield models are the most common tools used in fisheries management studies in Finland. In the research on whitefish stocks, both yield-per-recruit (Y/R) models (Auvinen 1987, I, II) and models based on cohort analysis or virtual population analysis (VPA) (Raitaniemi et al. 1995, Salonen et al. 1997, 1998, IV) have been used. Salojärvi (1992a) has analysed relationships between the spawning stock and recruitment in several whitefish stocks. The age-structured spreadsheet models used in the decision analysis approaches in articles V and VI are principally Y/R models, linked to an influence

diagram model (Chapter 4.3).

With Y/R models it is possible to assess how a change in fishing mortality or age of recruitment would affect the average yield, and at which rate of fishing the maximum yield would be achieved (I, II). An equilibrium state is assumed, where growth rate, recruiting age and age-specific mortalities are constant.

The basic material used in the Y/R analyses consisted of whitefish samples, fishing questionnaires, and daily records of fishermen's effort and catches (I, II, V, VI). From Lake Kemijärvi, in total 1250 whitefish were sampled from 1983–1985, from Lake Paasivesi 9700 whitefish from 1980–1988, and from Lake Lappajärvi 2500 whitefish from 1989–1993. Detailed descriptions of the samples by gear, fishermen's bookkeeping, and fishing questionnaires are presented by Heikinheimo-Schmid & Huusko (1987a), Heikinheimo-Schmid et al. (1987) and Heikinheimo-Schmid (1987) for Lake Kemijärvi, Heikinheimo-Schmid (1985a) for Lake Paasivesi, and Raitaniemi et al. (1995) for Lake Lappajärvi.

Whitefish were sampled from the catches of the most commonly used gear types, from both the commercial and subsistence fishery, so that

the material corresponded as closely as possible to the composition of the annual catch of the fishermen. The total length and weight of the whitefish were measured, sex was determined, and the gill rakers were counted from the outermost gill arch to determine the whitefish form. Scales taken from between the ventral fins were used for age determination. In Lake Lappajärvi, the operculum bones were also used (Raitaniemi et al. 1995).

The lengths of whitefish at earlier ages were back-calculated for the samples from Lake Kemijärvi and Lake Lappajärvi (I, V). In Lake Paasivesi, the growth of the whitefish was calculated from seine samples assuming that the seine does not select the most rapidly growing individuals as do the gill nets (II). For the whitefish from Lake Kemijärvi, software based on the method by Ricker & Lagler (1942, ref. Bagenal & Tesch 1978) was used for the back-calculation (J. Leskinen, unpublished). For Lake Lappajärvi (Raitaniemi et al. 1998), Monastyrsky's method was applied (Bagenal & Tesch 1978). The corresponding age-specific weights were calculated using the length-weight relationships estimated from the whitefish samples in question.

Table 3. The whitefish forms, and occurrence of vendace and brown trout in the lakes studied.

Lake	Native whitefish forms	Stocked whitefish forms	Vendace	Brown trout
Kemijärvi (I)	<i>C. l. wartmanni</i> (declined) <i>C. l. lavaretus</i> <i>C. l. pallasii</i> (declined)	<i>C. l. pallasii</i> <i>C. l. lavaretus</i> <i>C. l. fera</i> <i>C. peled</i>	yes	yes
Paasivesi (II)	<i>C. l. wartmanni</i> <i>C. l. pallasii</i> (declined)	<i>C. l. pallasii</i>	yes	yes
Vuokalanjärvi (IV)	? (sparse population of densely-rakered whitefish, originating from an earlier stocking)	Experimental stocking in 1987–1988: <i>C. l. pallasii</i> <i>C. l. wartmanni</i> <i>C. l. lavaretus</i> <i>C. l. fera</i>	yes (low density during the study period 1987–1992)	yes
Lappajärvi (V)	<i>C. l. nilssonii</i> ? (declined)	<i>C. l. pallasii</i>	yes	yes
Päijänne (VI, VII, Heikinheimo & Valkeajärvi 1998)	<i>C. l. wartmanni</i> <i>C. l. nilssonii</i> (declined) <i>C. l. pallasii</i> (declined)	<i>C. l. pallasii</i>	yes	yes

The catches per unit of effort (CPUE) for each gear type (I, II) were calculated on the basis of the daily catch records of the fishermen. The catches of gill nets were recorded by mesh-size class. The mesh-size classes were 27–33 mm, 34–40 mm and > 40 mm (bar length). Vendace gill nets (mesh sizes < 27 mm) were treated separately. In Lake Paasivesi (II), the CPUE data by year class was used for mortality estimation (Ricker 1975). The mortalities were calculated using the method by Robson & Chapman (1961) (I, II), or catch curves (Ricker 1975) and cohort analysis (Pope 1972) (IV, V, VI).

The yield-per-recruit for Lakes Kemijärvi and Paasivesi was calculated using the equations of cohort analysis (I, Gulland 1983, p. 105) and the method by Beverton and Holt (II, Ricker 1975, p. 251). The age-structured spreadsheet models used in articles V and VI were based on the equations of cohort analysis (Gulland 1983).

The implementation of the recommendations given in the 1980s for Lakes Kemijärvi and Paasivesi, and the results of the management measures are evaluated in this synthesis on the basis of reports on monitoring research or other literature. In Lake Kemijärvi, monitoring of the results of the compensatory fish stocking has been continued after the research project from 1982–1985 using the daily catch records of fishermen, a questionnaire on fishing and catches in 1991, and catch samples (Leskinen & Liekonen 1992, Lovikka & Liekonen 1993, Lapin Vesitutkimus Oy 2000). A plan for fisheries management in Lake Kemijärvi for the period from 1996–2000 was composed by Homanen & Liekonen (1996). In Lake Paasivesi, only the vendace stock has been monitored in the 1990s (Auvinen et al. 2000).

4.3. Age determination test

Age determination from scales has been found unreliable in many cases and several fish species including whitefish (Raitaniemi et al. 1998). To assess the validity of the age readings of whitefish with differing growth rates, samples were taken from two whitefish populations, one a slowly-growing, sea-spawning population (*C. l. widegreni*) from the Gulf of Bothnia, and the other the fast-growing migratory whitefish (*C. l. lavaretus*)

from the River Vantaanjoki (III). The readers aged 50 individuals from each population, using scales (4 readers) and otoliths (3 readers) separately. The detailed description of the handling of the ageing material is given in article III. The age determinations of different readers and ages determined from scales and otoliths were compared with each other. A small number of marked known-age (4+) whitefish from the River Vantaanjoki were available for evaluating the correctness of the age determination of the test sample.

4.4. Stocking experiment in Lake Vuokalanjärvi

To study the competitive abilities of different whitefish forms, and their suitability for stocking, an overdense whitefish population was created in Lake Vuokalanjärvi in 1987–1988 (IV) by stocking equal numbers of five different whitefish stocks (four forms): *C. l. fera* from Lake Inari, *C. l. lavaretus* from the River Kuusinkijoki, *C. l. wartmanni* from Lake Kermajärvi, *C. l. pallasi* from the Sotkamo lake system, and another *C. l. pallasi* stock from the River Koitajoki. All whitefish were tagged with coded wire tags for identification of the stock and stocking year. Sampling was based on experimental fishing with seine nets, trap nets and gill nets. The ages of the whitefish were known on the basis of tagging. In addition to the measurements mentioned above, the stomachs of the whitefish were sampled for the diet study, which is described in detail in article IV. The population sizes of the whitefish stocks were examined using cohort analysis.

4.5. Multispecies approaches

The fisheries management issues recently debated in Finland have concerned the multispecies effects of fishing, such as by-catches (Makkonen et al. 1996) and protection of endangered stocks (Salmi et al. 2000), conflicts between different fisher groups (Salmi & Auvinen 1998), and interactions between fish species (Vehanen et al. 1998). Obviously, more effective tools than single-species models are needed to handle these problems. Here, Bayesian influence diagram models were

The uncertainty in fisheries management is due to biological, economic and social factors (Charles 1994, Hildén 1997). Francis & Shotton (1997) and Hildén (1997) have presented thorough reviews on different types of uncertainty. In this thesis, attention is directed mainly at the biological sources of uncertainty. Socioeconomic aspects, such as the behaviour of the fishermen and economic interactions, were not included in these modelling approaches (V, VI, VII).

The interactions between fish species, such as predation and competition, have often been ignored in fish stock models (Hilborn & Walters 1992). The reason is probably that the effect of these factors has been considered as insignificant, or difficult to assess and control. Even if the importance of these parameters was recognized, the estimation of their values may be insurmountable or demand extensive sampling. Until the 1990s, there has also been a lack of suitable modelling software.

In the influence diagram models for Lake Lappajärvi (V, Fig. 5) and Lake Päijänne (Heikinheimo & Valkeajärvi 1998) the objective function was the benefit from whitefish and brown trout stocking, and in Lake Päijänne, the value of the catch of the native whitefish *C. l. wartmanni*. The decision variables were the mesh size restrictions on the gill-net fishery, fishing effort, and the stocking size of brown trout.

In the Lake Lappajärvi model (V, Fig. 5), the numbers of stocked whitefish and brown trout were modelled as deterministic variables, because these were based on obligations settled by the court, and the main interest in the study was directed at the effect of restrictions on gill-net fishing on the stocking result. The effect of the recreational value of brown trout fishing on management decisions was examined by using a recreational coefficient for the brown trout catch, with values from 1–10 (V). In the model for Lake Päijänne (Heikinheimo & Valkeajärvi 1998), the money available for the brown trout stocking was modelled as constant, and thus the stocking size affected the number of brown trout stocked.

The interactions between the fish species were taken into account by modelling the inverse dependence of the growth rate of whitefish on the

density of vendace as two alternative options (V). In the Lake Päijänne model, the positive effect of vendace density on the growth of brown trout (Niva & Julkunen 1998) was also modelled. The two alternative scenarios were then considered separately: dense vendace stock–slow growth of whitefish–rapid growth of brown trout, and vice versa.

The Lake Päijänne model (Heikinheimo & Valkeajärvi 1998), principally similar to that presented in article V, was then expanded to include the effects of fisheries management on vendace via predation by brown trout (VI). In article VI, only the low-density state of vendace is considered, because the main hypothesis was that predation might be able to maintain the low-density state. At high vendace densities, the effect of predation is small (Vehanen et al. 1998), because it is limited by the maximum consumption of the predators (Taylor 1984).

The Decision Programming Language DPL (1995) was applied to create the influence diagrams and to perform probabilistic calculus, linked with age-structured spreadsheet models in Windows Excel (Microsoft) to calculate the stock sizes and yield-per-recruit. The DPL model inputs the parameter values to the spreadsheet model, receives the results of the calculations, and then produces the probability distributions for the outcomes using the probabilities given for the alternative values of the probabilistic variables. A value sensitivity comparison was used to compare the effect of separate variables on the expected value of the objective function and on the decisions (V, VI).

The parameter values used in the influence diagrams were based on Raitaniemi et al. (1995) for Lake Lappajärvi (V) and on Valkeajärvi & Salo (2000), Koivurinta et al. (2000), Heikinheimo & Valkeajärvi (1998) and unpublished data by P. Valkeajärvi for Lake Päijänne (VI). Simple discrete probability distributions with three stages were used for the chance variables.

The most important question about what really causes the low-density periods of vendace, or subsequent recoveries, could not be solved with the influence diagram model (VI). Moreover, the influence diagrams were based on equilibrium spreadsheet models. With vendace, this is in many

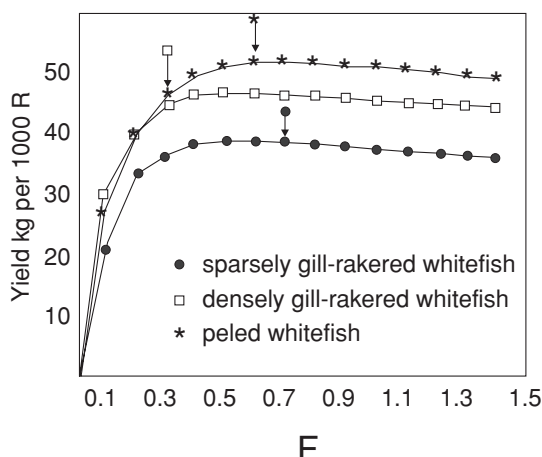


Fig. 6. Yield-per-recruit curves for the whitefish in Lake Kemijärvi (I). Instantaneous natural mortality (M) = 0.3; F = instantaneous fishing mortality; and the arrows indicate the rate of fishing from 1983–1985.

cases unjustified because of strongly varying recruitment, although during long periods of low vendace density the recruitment is maintained on a more steady level. Further, the influence diagrams were not able to handle feed-back mechanisms, which are common in the dynamics of fish stocks. To describe the effect of predation more realistically, and to include the assumed interactions between perch and vendace, dynamic modelling was applied to study the predation by brown trout and perch on vendace (VII). The data from Lake Päijänne (Valkeajärvi, unpublished, Valkeajärvi & Salo 2000) and Lake Puruvesi (Jaatinen et al. 1999, Vuorimies & Tolonen 1999, Auvinen et al., unpublished), and the software Powersim 2.51 for Windows were used for constructing the model and for simulations. Shepherd's (1982) equation was assumed for the stock-recruitment relationship of vendace, and the effect of different parameter values was examined by simulation. Types II and III of the functional response, described in detail in article VII, were used in simulations in the predation by brown trout and perch. The value of the half-saturation constant, which determines the steepness of the functional response curve, was based on the rough estimate for brown trout, presented in article VI. The same value was used for perch as well. Euler's integration method was used in simulations, with a time step of 0.01 years.

5. Results

5.1. Sustainability of the whitefish fisheries in the study lakes

5.1.1. Results of the Y/R analyses

The conclusion for all whitefish stocks studied in Lake Kemijärvi from 1983–1985 (I) was that a higher fishing effort would not increase the yield per recruit. The Y/R curves were not dome-shaped, which means that increased fishing would not have decreased the catches (Fig. 6).

In Lake Paasivesi (II), on the basis of the material sampled from 1980–1983, the recruitment of *C. l. wartmanni* to the fishery occurred at a suitable age to produce a maximum yield, but the recruiting age of *C. l. pallasii* should have been higher (Fig. 7), which means that the mesh size in the gill-net fishery should have been larger. The level of fishing mortality was at the right level for the *C. l. wartmanni* stock, but exceeded the optimum for *C. l. pallasii*, assuming no change in the recruiting age. The effect of fishing on the spawning stock of *C. l. wartmanni* was not considered here. During the period from 1980–1983, on which the Y/R analysis was based, the growth of the whitefish in Lake Paasivesi was more rapid, but was decelerated at the end of the decade (II), and as a consequence, the recruiting age of both whitefish forms was higher. In this new situation, more intensive fishing of *C. l. pallasii* was expected to result in a better yield from stocking, and the recruitment of *C. l. wartmanni* to the gill-net fishery was most probably incomplete (II).

5.1.2. Implementation of the recommendations given to fisheries management in Lake Kemijärvi (1983–1985)

The basis for the recommendations for whitefish fisheries management in Lake Kemijärvi (Table 4) were the results of the Y/R analysis (I), and the assumption that thinning out the dense whitefish stock and the perch and roach populations would accelerate the growth of whitefish (I). The slow growth was thought to be due to the reduced food resources, as a consequence of the strong water-level regulation, and the high stocking densities.

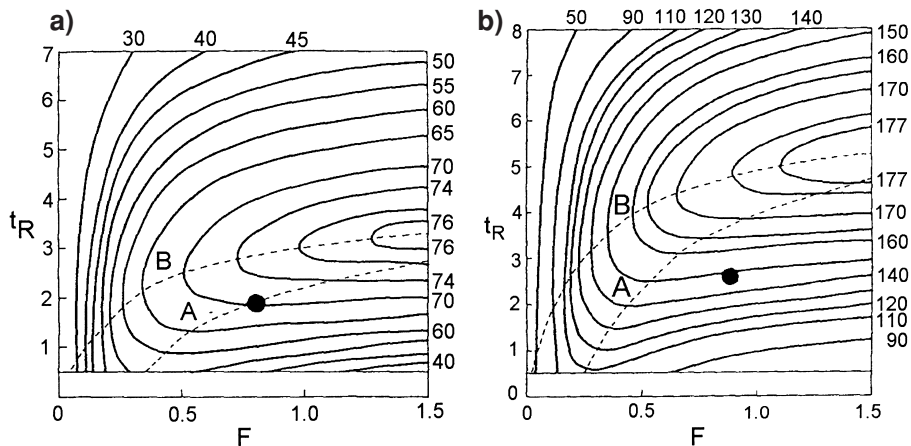


Fig. 7. Yield contour diagrams describing the yield-per-recruit for *C. l. wartmanni* (a) and *C. l. pallasii* (b) in Lake Paasivesi (Heikinheimo-Schmid 1985a). F = instantaneous rate of fishing mortality; t_R = mean recruiting age; ● = the situation during the study period 1980–1983; curve A = maximum yield for each recruiting age; curve B = maximum yield for each value of fishing mortality.

Table 4. The recommendations for fisheries management for whitefish in Lake Kemijärvi in the 1980s (I), their implementation and the results according to monitoring research.

Recommendation based on research from 1982–1985 (I)	Expected result (I)	Implementation in 1986–1999	Result	Probable reason for the observed result
1) Non-selective fishing gear such as seine and trap nets should be favoured	1), 2) and 3):	Number of seine and trap nets increased (c, e)	The catch of seine and trap nets mainly vendace, not whitefish (d, e)	Recovery of the vendace stock
2) Use of gill nets of small mesh size (30 mm bar length)	Thinning out dense whitefish stocks Thinning out perch and roach => accelerated growth of whitefish	No restriction on gill-net mesh sizes, small mesh sizes common (a)	The growth of whitefish has not been accelerated (b)	Abundant vendace stock, density of whitefish not decreased.
3) Use of pound nets allowed at least in professional fishing		Pound nets are not used (e)		
4) Stocking density of <i>C. l. pallasii</i> and <i>C. peled</i> should remain at the current level	Decreased total stocking density of whitefish, only plankton-feeding forms present => Accelerated growth of whitefish => better stocking results	<i>C. l. pallasii</i> mostly stocked in 1988–1994; <i>C. peled</i> only in 1989 (c) Stocking of <i>C. l. lavaretus</i> was stopped, but small numbers of <i>C. l. fera</i> have been stocked (c)	The composition of whitefish catch 1992: <i>C. l. fera</i> 11% <i>C. l. lavaretus</i> or <i>wartmanni</i> 29% <i>C. l. pallasii</i> 27% <i>C. peled</i> 32% (b) The growth of whitefish not affected (b)	Natural reproduction of <i>C. l. lavaretus</i> , <i>C. peled</i> washed down from the upstream reservoirs

Sources: a) Leskinen & Liekonen (1992), b) Lovikka & Liekonen (1993), c) Homanen & Liekonen (1996), d) Lapin Vesitutkimus Oy (2000), e) E. Liekonen, personal communication.

Although most of the recommendations were followed, the density of whitefish did not decrease and growth was not accelerated. The main reasons, discussed later in more detail, were the effect of vendace on whitefish, and the additional supply of whitefish to the lake from the upstream reservoirs. Moreover, the commercial fishery was directed mostly at vendace and was not able to thin out the whitefish stocks.

The recommendation on stocking densities for whitefish (I) has been followed (Table 4). More resources have been directed, instead of whitefish, to brown trout stocking with large smolts. There are no restrictions on gill-net mesh sizes. The most common mesh sizes in 1991 were a 36–45 mm bar length (51% of the effort with gill nets), and smaller mesh sizes (27–35 mm) were abundant as well (17%). The proportion of the > 45 mm gill nets was 31%. The whitefish catch with gill nets was distributed as follows: 27–35 mm 3390 kg; 36–45 mm 6820 kg, and > 46 mm 1140 kg. Only 200 kg of the whitefish was caught with seine nets (Leskinen & Liekonen 1992).

5.1.3. Development of the whitefish fisheries in Lake Paasivesi after the study period (1980–1983)

The following recommendations were given for the management of whitefish in Lake Paasivesi (II):

- 1) To raise the recruiting age of *C. l. pallasii*, the best minimum mesh size of gill nets would be 35 mm (bar length). More intensive fishing would result in a better yield from stocking.
- 2) To thin out the dense and slowly-growing *C. l. wartmanni* stock, trawling or seine netting is advantageous because of incomplete recruitment to the gill net fishery.
- 3) During the spawning period of *C. l. wartmanni*, this whitefish form can be caught selectively, and should then be intensively exploited with small-mesh gill nets.

The most common gill-net mesh sizes used in whitefish fishing in Lake Paasivesi during the study period from 1980–1983 were 27–33 mm. According to the Y/R analysis, the mean recruiting age of *C. l. pallasii* should have been as much as five years, which would have demanded a more

substantial restriction of the mesh size than the proposed minimum 35 mm. In Lake Lappajärvi, the recommendation for minimum mesh size was 45–55 mm (bar length), depending on the growth rate of *C. l. pallasii* (V). The proposal for Lake Paasivesi was related to the current situation, and in reality, it was apparently too cautious.

At the end of the 1980s, an abundant infection with *Triatophorus crassus* was reported in whitefish in Lake Saimaa, including Lake Paasivesi (Pulkkinen 1999), and the economic value of the whitefish collapsed as a consequence (T. Nurmio, Finnish Game and Fisheries Research Institute, personal communication). Stocking with whitefish (*C. l. pallasii*) was suspected to have caused or accelerated the infection. This led to a recommendation to avoid whitefish stocking, and therefore the stocking with whitefish was terminated in Lake Paasivesi. Hence, the whitefish stock in Lake Paasivesi currently consists only of the lake-spawning *C. l. wartmanni*. The abundance of vendace is a determining factor in the fishery. The long low-density period, started in the late 1980s, has continued in Lake Paasivesi although in other parts of Lake Saimaa the vendace stocks have recovered (Auvinen et al. 2000). Two trawlers are fishing in Lake Paasivesi, and one third of their catch was whitefish in 1999 (23 kg per hour). The whitefish stocks are not monitored in Lake Paasivesi. There are restrictions on trawl and gill-net fishing, aimed at preventing the recruitment overfishing of vendace, and protecting the endangered salmonid predators (H. Härkönen, Mikkeli Fisheries Centre, personal communication). In surface and mid-water gill nets, the minimum allowable mesh size is 65 mm (bar length). In the nearby Lake Savonselkä the minimum mesh size in bottom gill nets is 50 mm, with the exception of the spawning period of whitefish (*C. l. wartmanni*) from October 15 to November 15.

5.2. Responses of different whitefish forms to overdensity

The experimental stocking in Lake Vuokalanjärvi (IV) aimed at examining the differences between the whitefish forms in their responses in a competitive situation. Therefore, the stocking density was in total 132 fingerlings per ha, about three

times the highest recommended densities (Salojärvi 1992b). The hypothesis was that the strict competition would cause habitat and food segregation, and the sparsely gill-rakered forms would shift to a predominantly benthic diet, while the densely gill-rakered forms would live pelagically feeding on plankton. The differences in growth and mortality rates would reflect the competitive capabilities of the whitefish forms.

In the resulting dense whitefish population in Lake Vuokalanjärvi, the instantaneous rate of total mortality at the age of one to five was only 0.2–0.3 (IV). Fishing was ineffective because the whitefish were not recruited into the gill-net fishery of local fishermen in the first five years after stocking. Hence, the experimental fishing was the only cause of fishing mortality. The growth was slow in all stocks, but the *C. l. pallasii* stock from the River Koitajoki, the same lake system as Lake Vuokalanjärvi, showed more rapid growth in weight. However, the other *C. l. pallasii* stock from the Sotkamo lake system did not differ from the sparsely-rakered whitefish forms in growth rate.

The whitefish stocks differed in vulnerability to the gear types used in experimental fishing, which most probably reflects differences in their choice of habitat. However, there was no clear dependence between the gill-raker density and choice of pelagic or littoral habitat. The lake-spawning *C. l. wartmanni* stock from Lake Kermajärvi and the *C. l. pallasii* from Sotkamo were most abundant in the seine catch from the pelagic area, while both *C. l. pallasii* stocks were common in the trap nets, situated in more shallow areas. In gill nets, the proportion of the sparsely-rakered *C. l. fera* was higher than in the other gear types. The proportion of the migratory whitefish *C. l. lavaretus* from the Kuusinkijoki River was low in all gear types. The whitefish fed predominantly on zooplankton, but the sparsely-rakered forms *C. l. lavaretus* and *fera* showed a starting orientation towards benthic food from the age of three years onwards.

5.3. Management of mixed fishing of whitefish and brown trout

The management of mixed fishing of whitefish and brown trout means in practice that gill-net

fishing should be restricted. Restrictions on mesh sizes and fishing effort were both considered in the cases of Lake Lappajärvi (V) and Päijänne (Heikinheimo & Valkeajärvi 1998).

The management of mesh sizes is more effective, because it protects the particular size classes of the target and by-catch species from gill-net fishing.

Recommendations concerning gill net mesh sizes, based mainly on the influence diagram analyses for Lake Lappajärvi (V) and Lake Päijänne (Heikinheimo & Valkeajärvi 1998), are summarized in Fig. 8. Here, the brown trout is assumed to originate from stocking, and therefore the potential recruitment overfishing is not taken into account. The total benefit from stocking is the objective function. The recreational value of the brown trout catch with rods is assumed to be at least twice the price of the catch (recreational coefficient ≥ 2 , V). These cases represent common situations in Finnish lakes: the whitefish form most commonly stocked is *C. l. pallasii*, and the small-sized, pelagic *C. l. wartmanni* has a wide distribution (Kaukoranta et al. 1998). The exact mesh sizes to be recommended are case-specific and depend on the whitefish forms present and their growth rates. The lower limits of mesh size classes in Lake Lappajärvi were the following (bar lengths): small 35 mm, medium 45 mm, and large 55 mm. In Lake Päijänne, the mesh size (bar length) classes were: small ≤ 35 mm; medium 36–54 mm and large ≥ 55 mm.

The periodic variation in the growth of whitefish, apparently related to the density of the vendace, provided different recommendations for the periods of dense and sparse vendace stock, with slow and rapid whitefish growth, respectively. The trap net ("pound net" in the article V) fishing of whitefish enables the setting of the minimum mesh size of gill nets more advantageously for brown trout, because the whitefish fishery is ensured by the trap nets even during a slow-growth period.

The influence diagram analysis revealed that the effect of mesh size regulation may be minor compared to the wide probability distribution of the expected yield from stocking with whitefish and brown trout (V, Heikinheimo & Valkeajärvi 1998). For instance, in the northern part of Lake Päijänne, the restriction of gill net mesh sizes

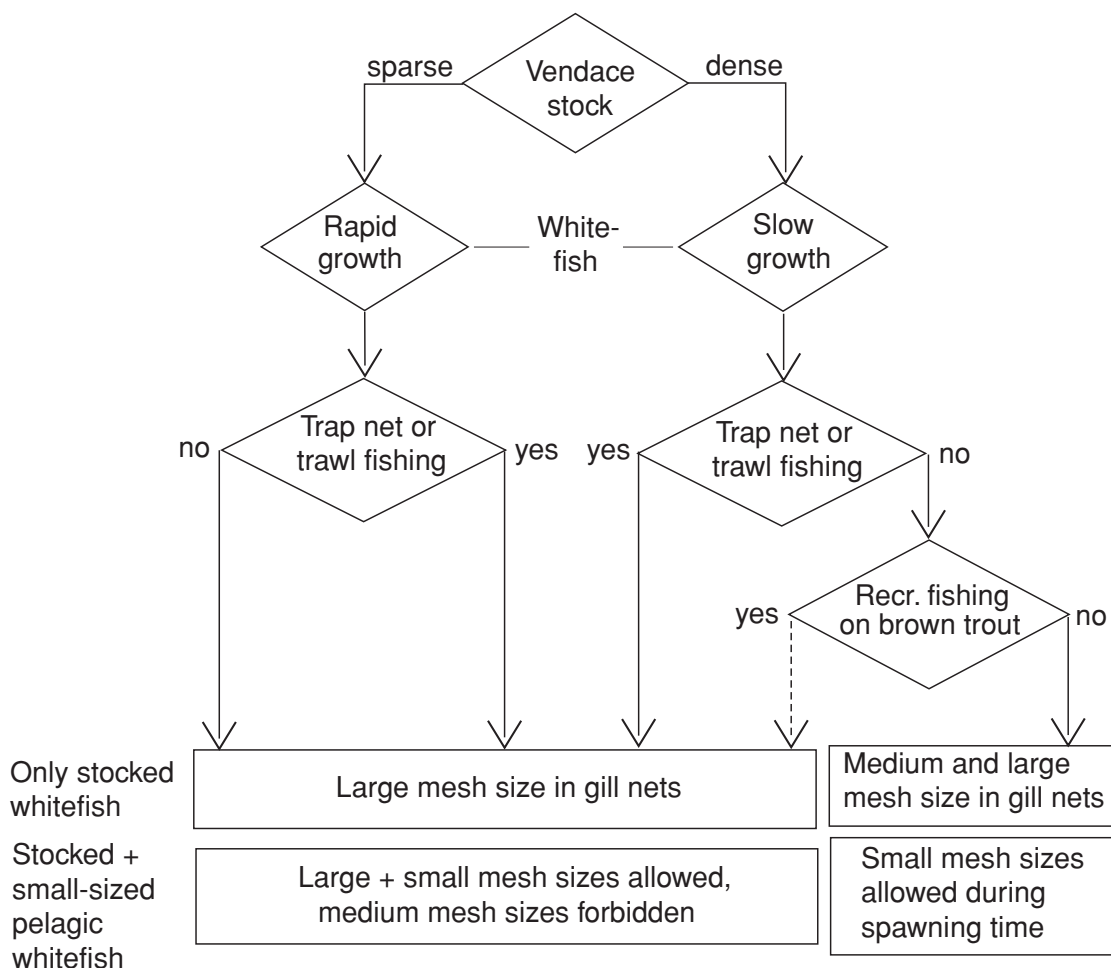


Fig. 8. Flow chart summarizing the recommended management of gill-net mesh sizes in the mixed fishing on whitefish and stocked brown trout (I, II, V, Heikinheimo & Valkeajärvi 1998). The arrow with a dashed line indicates that the total benefit is larger in this alternative, but the probability of the unprofitable stocking of whitefish would be 70% (V).

(medium mesh sizes forbidden) would increase the benefit from whitefish and brown trout stocking by half during an abundant vendace stock (Fig. 9, Heikinheimo & Valkeajärvi 1998). However, the difference between the expected values is only 10% of the overall range of the probability distribution. In practice, this means that if the mesh size restriction came into force, the effect would be difficult to detect in the short term because of the extensive random variation. In the case of Lake Päijänne, in spite of the wide distribution of the expected yield, the parameter uncertainty did not affect the decisions concerning the fisheries man-

agement. The effect of mesh size regulation on the size distribution of the brown trout in the catch was clearer than on the yield from stocking. For instance, the proportion in the catch of small brown trout (less than 1 kg in weight) would decrease as a consequence of the recommended restriction (Heikinheimo & Valkeajärvi 1998). In Lake Lappajärvi (V), the estimated effect of mesh size restriction was larger, because the planned regulation was different (a minimum mesh size instead of forbidden medium mesh sizes) and the small-sized *C. l. wartmanni* was lacking in Lake Lappajärvi.

Fig. 9. Cumulative probability distributions of the total benefit from whitefish and brown trout stocking for two scenarios in the mesh size regulation of gill nets in the northern part of Lake Päijänne (Heikinheimo & Valkeajärvi 1998). The vertical lines show the expected values.



5.4. Indirect effect of the management of gill-net fishing on vendace

In spite of the expected positive effect of the planned mesh size restriction on the composition of the brown trout catch in Lake Päijänne (Heikinheimo & Valkeajärvi 1998), the predation on vendace would not be affected markedly (VI). Similar to the yield from stocking, the expected decrease in the vendace catch, and in the spawning stock density due to the mesh size restriction would be less than 10% of the range of the probability distributions. A decline by half in the fishing effort with gill nets would have a larger effect. The stocking size of brown trout would most probably not affect the predation on vendace, because the higher price of the large smolts would accordingly decrease the stocking density (VI).

5.5. Significance of brown trout and perch as predators of vendace

The simulations with the dynamic model (VII) showed that, given the assumptions of the model, long low-density periods in vendace stocks can be produced as a consequence of predation on young-of-the-year vendace. The results supported the hypothesis that perch may play a decisive role

in maintaining the low-density state in vendace stocks, even if it was most probably not the primary cause of the collapses. On the contrary, the assumptions that stocking with brown trout would be significant were not supported.

The dynamic model, where predation by perch was included, revealed that the estimated S/R relationship and functional response are crucial when the effect of predation is studied (VII). Two types (II and III) of functional response (Taylor 1984) were used in simulations, with the same value for the half-saturation constant (Fig. 10). The type II response in predation by brown trout and perch was able to produce practically an extinction of vendace by high predation pressure, although in the simulations the vendace stock was able to recover even from very low levels when the density of predators decreased. In the natural environment, this is hardly possible because there must be a density limit needed for successful reproduction (Myers et al. 1995).

With the type III functional response and the nominal dome-shaped S/R curve, brown trout stocking had a clearer effect on the vendace stock density than with the type II response (Figs. 11 and 12). On the other hand, there was only a small difference between the case with perch predation only and the case with both predators. The vendace stock did not fall to zero in any case, even if the

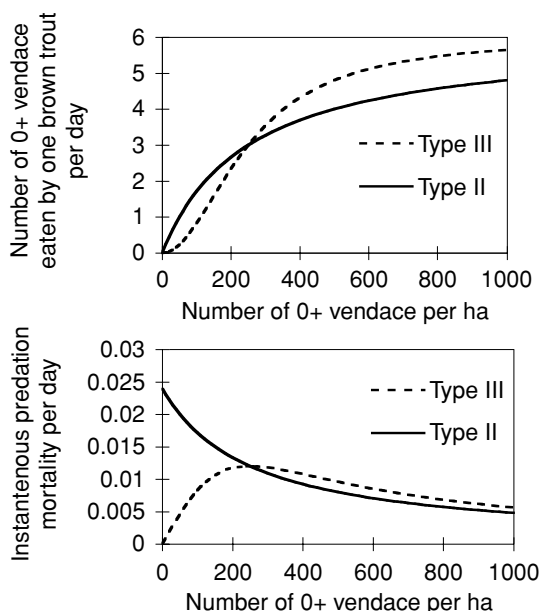


Fig. 10. The functional response curves of types II and III used in the model for the predation by brown trout on 0+ vendace, and the corresponding instantaneous rates of predation mortality (below). Half-saturation constant (D) = 250 0+ vendace per ha in both types, maximum consumption 6 vendace per day (VII).

simulation was started from low densities. With flat S/R curves the equilibrium densities of vendace were almost equal irrespective of the type of functional response, with the exception that with the type II response low starting values led to zero output. The overall picture of the behaviour of the model with the type III response was more stable than with the type II response, which in most cases produced an oscillation in the population size (Fig. 11). With the type III response, the oscillation converged towards an equilibrium point for each case of predation (Fig. 12).

5.6. Sources of uncertainty in the models

5.6.1. The biological sources of uncertainty

On the basis of sensitivity analyses, the main biological sources of uncertainty in the whitefish

model for Lake Lappajärvi (V) were the natural mortality of whitefish and the post-stocking survival of the whitefish fingerlings, but only natural mortality affected the decisions on fisheries management. In the Lake Päijänne model (Heikinheimo & Valkeajärvi 1998), none of the variables in the whitefish model, varying within the assumed limits, were able to change the decisions. In the brown trout–vendace model for Lake Päijänne (VI), the density of the spawning stock of vendace was most sensitive to the year-class strength and natural mortality of vendace, and through the predation effect, on the post-stocking survival of the brown trout young. The estimated uncertainty in the value of the half-saturation constant in the functional response affected the expected value of the spawning stock density about 7% (VI).

5.6.2. Recreational value of brown trout fishery

In the Lake Lappajärvi model (V), the effect of the recreational value of brown trout fishing on fisheries management decisions was studied by sensitivity analysis. When the recreational value was modelled as a coefficient of the price of the brown trout catch with rods, the output of the model was sensitive to this parameter between values 1 and 2, while larger values did not change the decisions. This means that for values ≥ 2 of the recreational coefficient, the decisions most favourable for brown trout (large mesh sizes) will be chosen in the analysis. In some cases, whitefish stocking would then become unprofitable (Fig. 8).

5.6.3. Age determination as a source of error

In the whitefish stocks used in the age determination test (III), scales alone were obviously not reliable enough for age determination irrespective of the growth rate. The resulting age compositions of the samples were clearly dependent on the reader, and this reflects to the mortality estimates. Otoliths alone were found to be more reli-

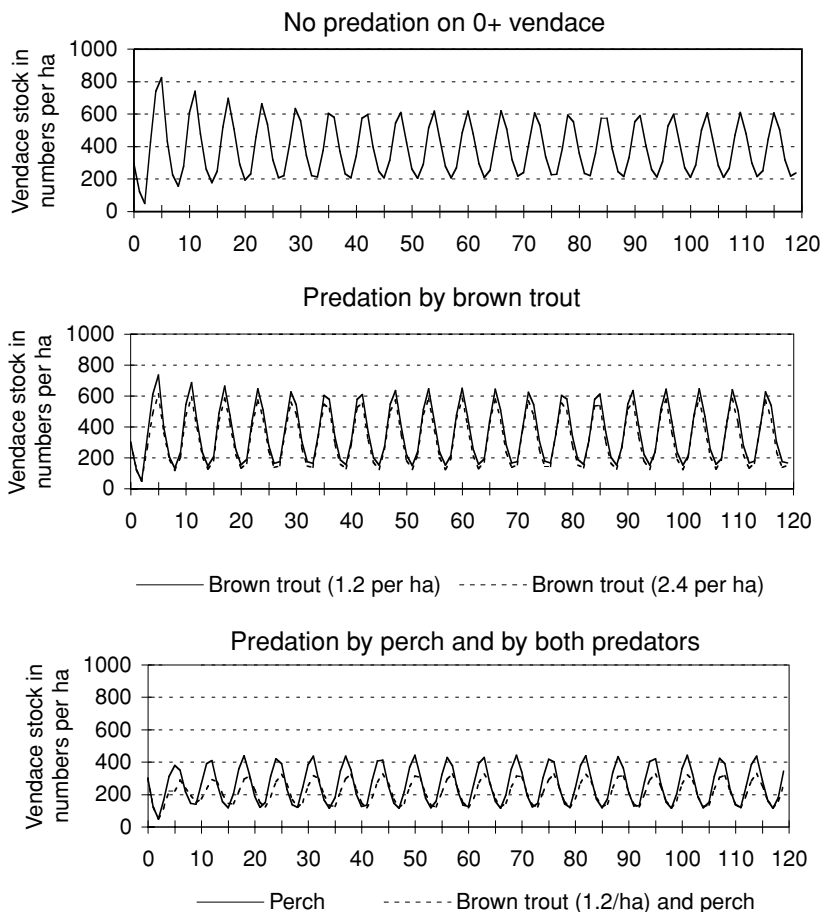


Fig. 11. Results of model simulations for 120 years with constant parameter values, assuming the type II functional response and the nominal stock-recruitment relationship ($a = 330$, $b = 3$). Densities of the vendace stock (one-year-olds and adults) for different predation scenarios: no predation on 0+ vendace, predation by brown trout only, predation by perch only, and predation by both species.

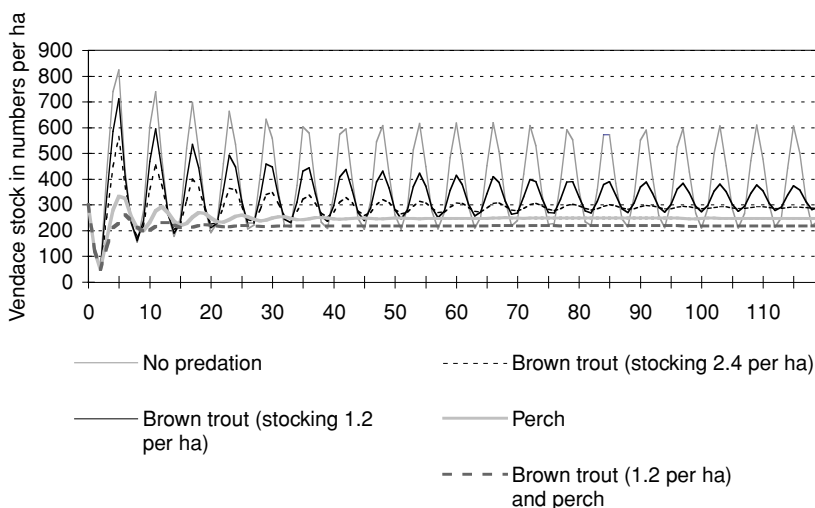


Fig. 12. Results of model simulations (VII) with constant parameter values assuming the type III functional response and the nominal stock-recruitment relationship ($a = 330$, $b = 3$). Densities of the vendace stock (one-year-olds and adults) for different predation scenarios: no predation on 0+ vendace, predation by brown trout only, predation by perch only, and predation by both species.

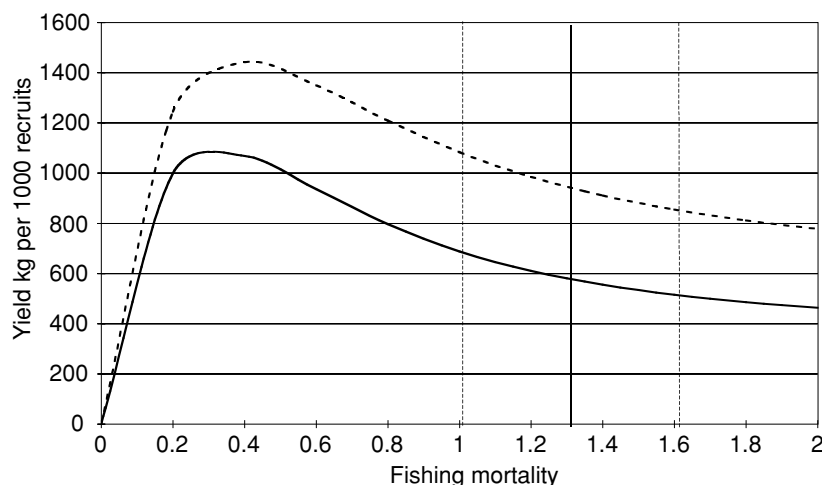


Fig. 13. Yield-per-recruit curves for the stocked migratory whitefish (*C. l. lavaretus*) in the Gulf of Finland, and the effect of uncertainty in the age determination on the mortality estimate. The curves show the yield per 1000 three-year-old recruits by minimum gill-net mesh sizes of 45 mm bar length (solid curve) and 50 mm (dashed curve). Vertical lines indicate the current rate of fishing mortality: solid line according to the age determination, and dashed lines for the minimum and maximum values when the uncertainty recorded by the reader was taken into account (Heikinheimo & Mikkola, unpublished).

able than scales alone (III).

The possibility to end up, due to ageing errors, with erroneous conclusions regarding fisheries management on the basis of a Y/R model depends on the form of the Y/R curve and on the current fishing mortality. According to unpublished data (Heikinheimo & Mikkola), the uncertainty in age determination recorded by the reader caused an uncertainty of $\pm 20\text{--}25\%$ in the estimate of the total mortality rate (Z) of the migratory whitefish from the Gulf of Finland, which was reflected in the estimate of the rate of fishing (Fig. 13). This did not affect the conclusion on the management of fishing, because both the minimum and maximum values of the estimated current fishing mortality were situated on the descending right limb of the Y/R curve, far from the optimum. This was the case for both rapid (Fig. 13) and slow growth rates observed in this stock. In this case, only growth overfishing was considered, because the population is maintained by stocking.

Principally, the ageing error in slowly-growing populations causes an overestimation of mortality, because old fish are thought to be younger, and thus the age distribution becomes steeper. In rapidly-growing populations, the opposite could occur because of false rings between real annuli (III).

6. Discussion

6.1. Sustainability of the multiform whitefish fisheries

Rapidly-growing whitefish, such as *C. l. pallasii*, are vulnerable to growth overfishing in lakes with no mesh size restrictions on the gill-net fishery (II, V, Heikinheimo & Valkeajärvi 1998). On the other hand, a large minimum mesh size may lead to underexploitation of pelagic, small-sized whitefish, and in extreme cases to dwarfing (Amundsen et al. 2000, IV). In lakes with native pelagic whitefish stocks and stocked rapidly-growing *C. l. pallasii* stocks the sustainability of the exploitation, and moderate result from stocking, can be ensured with suitable mesh size restrictions on gill nets (V, Heikinheimo & Raitaniemi 1998). Protection of native *C. l. nilssonii* or *C. l. pallasii* stocks from recruitment overfishing would demand special attention. The river-spawning *C. l. pallasii* has only a few reproduction areas left because of the dredging and damming of the rivers (Kaukoranta et al. 1998). The distribution of *C. l. nilssonii* is obscure, because some lake-spawning stocks are difficult to classify as either of the two forms, *C. l. nilssonii* or *wartmanni*. An example of recruitment overfishing in whitefish is the

C. l. nilssonii stock in Lake Päijänne (Valkeajärvi 1987). The small-sized *C. l. wartmanni* has been the main target of the whitefish fishery, and hence the more rapidly growing *C. l. nilssonii* has been subjected to recruitment overfishing. Generally, recruitment overfishing is probable in those lakes, where whitefish stocks exhibit differing growth rates and the fishing is directed at the slowly-growing stock.

In managing the gill-net fishing of whitefish, there are better opportunities to apply mesh size restrictions in lakes where the small-sized pelagic whitefish is caught commercially with seine nets, trawls, or trap nets (I, II, V). Moderate harvesting of the pelagic stock is then ensured, and the mesh size restrictions can be set to enhance the rapidly-growing whitefish. On the other hand, the results from Lake Päijänne indicated that trawl fishing tends to decrease the yield from stocking with *C. l. pallasii* by taking young whitefish (Heikinheimo & Valkeajärvi 1998), and if the mesh size of gill nets was restricted in this situation, the resulting increase in the whitefish catch almost exclusively benefits the trawlers. In practice, the decisions on management are mostly compromises, and the goal of maximizing the whitefish yield will not be achieved. Restriction of trawl fishing may not be advisable, if the commercial fishery on whitefish is to be maintained. Whitefish is a suitable target species as an alternative for vendace, when the fluctuations of vendace stocks seasonally weaken the profitability of the commercial fishery (Sipponen et al. 1999).

Density-dependent growth may lead to the dwarfing of the whitefish if the fishing mortality is low, especially when combined with high stocking density (Salojärvi 1988, Salonen et al. 1998, IV). A typical feature is an accumulation of old, small-sized and heavily parasitized fish (Amundsen et al. 2000). Thinning the dense whitefish stock is laborious and the catch is not desired (Sarjamo et al. 1989). Mass removal of the dwarfed whitefish is needed in such cases, and the best tools in such trials have been trawls, seine nets and trap nets. The trap net was found to be the most suitable for dense whitefish stocks (Mutenia 1991, Ahonen 1991, Mutenia et al. 1995), and positive results were obtained, for instance, in the Lokka and Porttipahta reservoirs (Salonen & Mutenia 1992, Salonen et al. 1997). In these reservoirs,

unexpectedly, the introduced *C. peled* started to reproduce naturally in 1986, which led to an overdense stock. Effective fishing with trap nets and trawls, started in 1990, thinned the stock out, and the situation was normalized within five years. During this period, the stocking was intermitted as well (Salonen et al. 1997). However, in naturally reproducing populations, the situation easily returns to the previous state when effective fish removal has ceased (Amundsen et al. 2000).

In Lake Inari, there are both normally growing and dwarf forms of *C. l. wartmanni* and *C. l. fera* (Toivonen 1960, Mutenia & Salonen 1991). The dwarf *C. l. wartmanni*, called "reeska", resembles vendace in its living habits and is an important target of trawl and seine fishing. The other dwarf whitefish (*C. l. fera*) "rääpy" dwells near the bottom and is undesired as catch (Toivonen 1960). Thus, dwarfing is one of the life strategies of whitefish in the natural environment.

In Lake Vuokalanjärvi, all whitefish forms introduced responded to the overdensity by slow growth, irrespective of the gill-raker density (IV). The stocks belonging to the same form (*C. l. pallasii*) differed in their behaviour and growth rate. Moreover, the *C. l. pallasii* from Sotkamo and *C. l. wartmanni* from Lake Kermajärvi were closer to each other in habitat choice and growth than the two *C. l. pallasii* stocks. This confirms that the behaviour or stocking success of whitefish cannot be predicted on the basis of the whitefish form in question. In fisheries management, whitefish stock is a more suitable unit of classification than form. Introducing whitefish stocks from distant areas may lead to poor results in stocking, in particular, because the stock is adapted to different circumstances in terms of food resources and fish assemblage (IV).

6.2. Evaluation of the recommendations for Lakes Kemijärvi and Paasivesi

In Lake Kemijärvi (I), a key problem in the whitefish fishery during the study period (from 1983–1985) was the high stocking density. Because the whitefish stocked in the upper parts of the water system partly washed down to the lake, the real stocking density may have been as much as 30 fingerlings per ha (I). The growth of all

whitefish in Lake Kemijärvi was slow in comparison, for instance, with the whitefish in the Lokka and Porttipahta reservoirs, or with growth data from the 1960s, before the start of water level regulation in Lake Kemijärvi. Much of the stocked migratory whitefish migrated downstream out of the lake (I, Heikinheimo-Schmid & Huusko 1987b, 1990). Changes in the littoral fauna caused by water level regulation affect mainly sparsely gill-rakered whitefish which are specialized for this food type (I). The regulation of the water level causes erosion in the littoral zone and negatively affects many bottom animals important as fish food, such as large-sized insect larvae and nymphs, and molluscs (Heikinheimo-Schmid 1985b, I). In Lake Kemijärvi, the densely-rakered whitefish forms showed a better growth rate and almost no downstream migration (Heikinheimo-Schmid & Huusko 1987b, 1990). From Lake Oulujärvi, both stocked *C. l. pallasii* and the native lake-spawning whitefish migrated downstream but there was no marked effect on the population size (Hyvärinen et al. 1992).

The yield from stocking in Lake Kemijärvi was only 10 kg per 1000 stocked fingerlings (I). The recommended stocking density (I) was less than 10 per ha annually, which is in accordance with the guidelines given by Salojärvi (1992b). In Lake Kemijärvi, the density of whitefish gill nets (other than vendace gill nets) was 0.2–0.4 per ha.

In 1991, the whitefish catch per fishing household was on the same level (9.6 kg) as in 1980 (8.8 kg), the year 1982 being an exception (4.7 kg) (Homanen & Liekonen 1996). The same trend was found in the total catch from Lake Kemijärvi. In 1982, fishing effort was low because of a sparse vendace stock and high mercury content found in pike (Heikinheimo-Schmid & Huusko 1990).

Lower stocking density in the 1990s and the shift to densely-rakered whitefish forms in stocking did not result in the anticipated benefits because Lake Kemijärvi is constantly affected by the whitefish stocks in the upstream waters. Furthermore, the feeding conditions for sparsely-rakered whitefish are still poor (I), and the abundant vendace stock probably competes for food with the plankton-feeding whitefish. The growth of the whitefish was not accelerated in spite of the declined stocking density (Lovikka & Liekonen

1993, Lapin vesitutkimus Oy 2000). Currently, there are 11 seine nets and five trap nets used in Lake Kemijärvi (E. Liekonen, Lapland Fisheries Centre, personal communication). However, fishing effort with trawls and trap nets is directed mainly at vendace and cannot thin out the whitefish stocks.

The proportion of sparsely gill-rakered and peled whitefish in the catch in 1992 was large although the densely gill-rakered form *C. l. pallasii* was mostly stocked (Table 4.). Obviously, the migratory whitefish *C. l. lavaretus* originated from natural reproduction (I), and the peled whitefish from the large upstream reservoirs Lokka and Porttipahta, where the unexpected natural reproduction of the peled whitefish produced overdense stocks (Salonen & Mutenia 1992). From 1997–1999 the proportion of peled was already smaller (< 20%) than that of *C. l. pallasii* (44%) (Lapin vesitutkimus Oy 2000).

Currently, whitefish is not especially significant to the commercial fishery in Lake Kemijärvi, pike and vendace being the main target species. From 1997–1999, the proportion of whitefish in the fishermen's catch, according to the daily book-keeping of 11 fishermen, was only 2% (8% in 1991, Leskinen & Liekonen 1992). The main species in the catch were pike (38–52%) and vendace (18–39%) (Lapin vesitutkimus Oy 2000).

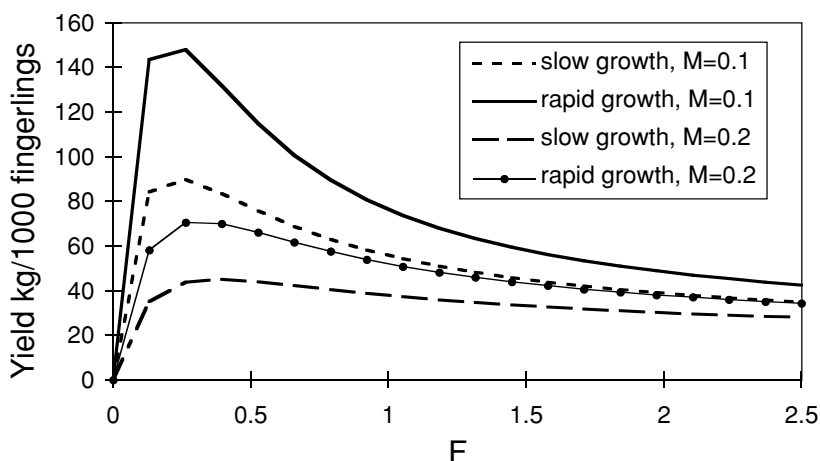
In Lake Paasivesi, the annual stocking density of whitefish in the 1980s was not too high compared with the guidelines of Salojärvi (1992b), about 6 fingerlings per ha (II), but the yield from stocking was low, 20–30 kg per 1000 fingerlings. The number of gill nets was 0.03–0.07 per ha for the whole lake, but gill-net fishing was concentrated in the nearshore area. The factors that affected the result of stocking were most probably the oligotrophy of the lake, the abundance of vendace and the native whitefish, and fishing with small mesh sizes.

6.3. Sources of error in the yield-per-recruit analysis

6.3.1. Uncertainty in the natural mortality rate

The natural mortality in fish stocks is a parameter that is greatly dependent on environmental cir-

Fig. 14. The effect of natural mortality and growth rate on the form of the Y/R curve, exemplified by the stocked *C. l. pallasii* in the southern part of Lake Päijänne (Heikinheimo & Valkeajärvi 1998). M = instantaneous natural mortality, F = instantaneous fishing mortality.



cumstances and that is difficult to estimate (V, VI). The value of natural mortality may greatly affect the conclusions regarding the state of the stock and the effect of fishing (Hildén 1997).

In the yield-per-recruit (Y/R) analysis the value of instantaneous natural mortality (M) affects the form of the curve describing the relationship between fishing mortality and yield (Fig. 14). The value of natural mortality is often assumed to be constant during the whole life of the fish, because the variation of this parameter is not exactly known. However, it is more plausible that the mortality is high in the early larval and juvenile phases, or immediately after stocking, and lower in the age groups recruited to the fishery (Salojärvi 1992a), because natural mortality depends on the size of the fish. Thus, using a constant natural mortality during the whole life of the fish tends to overestimate the natural mortality in the recruited age groups.

The natural mortality in young fish can be expected to vary strongly because it is sensitive to available food resources, density of predators and environmental factors. In Lake Kallioinen, the instantaneous natural mortality of whitefish, assumed as independent of age, varied from 0.07–0.3 by year class (Salojärvi 1992a). In Lake Kiantajärvi it was 0.12 on the average, and in Lake Oulujärvi 0.25 (0.11–0.37). The mortality caused by transportation and stocking stress, and post-stocking mortality in the lake were included in these estimates. The values of mortality were based on known amounts of stocked fish and numbers of fish caught by fishing annually (Salojärvi

1992a). Hence, the average natural mortality in the recruited age groups may have been 0.1–0.2 at its highest.

In the Y/R analysis for the whitefish in Lake Kemijärvi (I), for instance, the value for natural mortality was set at 0.3, which was generally used in whitefish research during that time, but was a high estimate according to more recent knowledge (Salojärvi 1992a). If the natural mortality was lower in reality, the fishing mortality in Lake Kemijärvi would have been higher than the estimate, which was based on the total mortality minus the natural mortality. In this case, the maximum yield would have been higher and the Y/R curves more dome-shaped. This would have strengthened the conclusions, because then a higher fishing effort would have even decreased the yield per recruit.

In Lake Paasivesi (II), the value of the instantaneous natural mortality in the analysis was 0.3 for *C. l. wartmanni* and 0.2 for *C. l. pallasii*. For *C. l. pallasii*, a lower value of natural mortality would have strengthened the conclusions, too: increase in the fishing effort had lowered the yield during the period of more rapid growth (1980–1983). For the slowly-growing *C. l. wartmanni*, this would not have caused any essential change.

The Y/R analysis is more realistic with age-specific values of natural mortality. In the Lake Lappajärvi model (V), we assumed that on the average 55% of the stocked whitefish fingerlings died before being recruited to the fishery, but with large variation, from 40–70%. In the recruited age groups the natural mortality was estimated at 0.1

on the average (from 0.05–0.15). In addition, a higher value of natural mortality was used in the case of slow growth (coefficient 1.5). According to the analysis, the value of natural mortality affected the decisions on fisheries management, such as minimum mesh size of gill nets and the recommended level of fishing effort with trap nets and gill nets. Thus, the uncertainty in the value of natural mortality, due to both natural variation and imperfect knowledge, should be taken into account in the management advice.

6.3.2. Age determination as a source of error

Our results confirmed that the age determination of whitefish from scales only is in many cases not reliable enough (III). Most problematic are very slowly or exceptionally rapidly growing whitefish. The correctness of the age determination is crucial in fish stock assessment, because it is the basis for both growth and mortality estimates. Even a fairly small proportion of erroneous age determinations can lead to a misleading estimate of age distribution (Raitaniemi et al. 1998). The estimation of growth rate is not as sensitive to incorrect age determination as is age distribution (Raitaniemi et al. 1998).

The uncertainty in age determination can be taken into account in the fish stock models if the reader records the potential range of the age in uncertain cases. However, if there were errors not detected by the reader, the consequences are difficult to predict. Systematic errors can be expected to be more fatal than random errors. Ageing errors may, for instance, mask variation in year-class strengths, and stock-recruitment relationships (Hilborn & Walters 1992).

In the rapidly-growing migratory whitefish from the Gulf of Finland, the age determination test (III) revealed that false rings between the annuli had led to underestimation of growth and mortality. After corrected age determination, by using known-age marked individuals and operculum bones and otoliths in addition to scales, the Y/R analysis indicated growth overfishing (Fig. 13), which was not recognized earlier due to biased age distribution (Heikinheimo & Mikkola, unpublished).

According to Salojärvi (1989), age determi-

nations based on the scales of the whitefish from Lake Oulujärvi were reliable. This conclusion was based on a test using tagged whitefish of a known age. In Lakes Kemijärvi (I) and Paasivesi (II), ageing errors could have occurred in the slowly-growing populations, if not all annuli were detected in old fish. In exploited populations, however, the proportion of old individuals is so small, that serious errors in the Y/R analysis are not probable. Most important is the correct age determination of those age groups that are abundant in the catch.

In Lake Lappajärvi, operculum bones were used in addition to scales, and tagged known-age individuals could be used to check the determinations (Raitaniemi et al. 1995). Thus, there were most probably no significant ageing errors.

The most important measures for avoiding ageing errors in whitefish are the following (III):

- 1) Use of several objects in the age determination, such as operculum bones and otoliths in addition to scales.
- 2) The readers should be experienced, and specialized in certain populations, because e.g. false rings are often typical to the population.
- 3) Use of known-age individuals, provided e.g. by stocking tagged whitefish fingerlings, to check the determinations.

6.3.3. Relevance of the equilibrium assumption in whitefish

The estimates of growth and mortality rates are the basis on which the fish stock assessment and management advice are founded, and mostly an equilibrium state is assumed. In reality, this is seldom true in the whitefish populations, which exhibit strong compensatory mechanisms in population regulation (Salojärvi 1992a) and are responsive to environmental disturbances or changes in interspecies interactions.

The equilibrium Y/R models do not account for the density-dependent growth of whitefish, and this may lead to erroneous conclusions about growth overfishing in some cases. A recommended high minimum mesh size in gill nets could cause a deceleration of growth in reality. Similarly, although the models based on an equilibrium assumption (V, Heikinheimo & Valkeajärvi

1998) indicate that trawl or trap net fishing decreases the catch of whitefish, this may not be true in cases where growth is accelerated by a decreasing density in the stock.

There are several examples of density-dependent growth in whitefish (Salojärvi 1992a, IV), although it was not found in Lakes Paasivesi (II) and Lappajärvi (Raitaniemi et al. 1995). For instance, a high stocking density has caused a deceleration of growth in whitefish (Salojärvi 1988, Salonen et al. 1998, IV), or, effective fishing has thinned out the whitefish stock and led to a better growth rate (Healey 1980, Salojärvi 1992a, Valkeajärvi 1992, Salonen et al. 1997).

Besides growth, the mortality of whitefish may be density-dependent. The whitefish stocking in Lake Lappajärvi in 1985 produced a poor result, and the stocking density was that year exceptionally high (36 fingerlings per ha). The mechanism was most probably an increased mortality of the whitefish young, or downstream migration (Raitaniemi et al. 1995). According to Salojärvi (1988) the natural mortality of whitefish in Lake Peranka increased markedly during high stock density. Compensatory mortality was probable in Lake Kallioinen as well, but was not observed in Lake Oulujärvi (Salojärvi 1992a).

Interspecific competition influences the growth of whitefish as well, and thus, alterations in the populations of other species may cause changes in the parameter values on which the management advice is founded. Vendace is the most important competitor of pelagic whitefish (Svärdson 1976). The competition with vendace was apparent in Lakes Paasivesi (II) and Lappajärvi (Raitaniemi et al. 1995). In Lake Paasivesi, the growth of whitefish, especially of *C. l. wartmanni*, was slower during a dense vendace stock (II). In Lake Lappajärvi, the growth of the stocked whitefish (*C. l. pallasii*) accelerated in all year classes, when the dense vendace stock collapsed (Raitaniemi et al. 1995, 1999). In the lower part of the Sotkamo lake system, the growth of the local whitefish was retarded in the 1980s. In that case, both the effective stocking with whitefish or increased density of vendace may have affected the growth (Salojärvi & Huusko 1990). Whitefish may react to an abundant vendace stock by withdrawing from the pelagic zone, which was reported, for instance, in Lake Päijänne (Valkeajärvi 1992).

Food competition between whitefish and benthos-feeding species, such as perch (*Perca fluviatilis* (L.)) and roach (*Rutilus rutilus* (L.)), is presumable but difficult to prove. According to Langeland & Nøst (1994), the size of the whitefish stock decreased and the composition of their diet changed due to the introduction of roach into the lake. Raitaniemi et al. (1999) reported that the growth rate of whitefish in different lakes is connected to the abundance of roach. Perch and roach may live pelagically (Horppila et al. 1997), especially when vendace or pelagic whitefish stocks are sparse (Valkeajärvi 1992). Smelt (*Osmerus eperlanus* (L.)) is a potential competitor, too (Sterligova 1979).

6.4. The concept of adaptive management

The examples of Lakes Kemijärvi (I), Paasivesi (II) and Vuokalanjärvi (IV) indicate that no universally applicable guidelines can be given for the management of the whitefish fishery, which is affected by large uncertainties and changes in environmental factors and species interactions. In the cases of Lake Kemijärvi (I) and Lake Paasivesi (II), unexpected changes in the environment lead to the irrelevance or ineffectiveness of the management advice given. These changes, the natural reproduction of *C. peled* in the reservoirs upstream from Lake Kemijärvi, or the infection by *Triaenophorus crassus* in Lake Paasivesi would not have been possible to predict. Here, the need of continuous monitoring and a flexible decision-making system in fisheries management is obvious.

Adaptive management has proved to be effective for whitefish (Müller & Bia 1998). The concept of adaptive management means a flexible adaptation of the fisheries management policy to changing situations in the face of uncertainty (Hilborn & Walters 1992, Müller & Bia 1998). Passive or active policies may be applied, the former being more conservative and suitable for systems with small uncertainties. The active policy may imply even deliberately excessive probing and experimentation in harvest schemes for uncertain fisheries systems in order to learn more about the system's reaction (Walters & Hilborn 1976, Hilborn & Walters 1992). Alternative models are constructed and decision analysis is used

for the identification of a suitable policy that offers possibilities to learn by probing but is cautious enough to prevent long-term overfishing (Hilborn & Walters 1992).

In the whitefish fishery, rapid changes in the management strategy may be necessary. The management measures are then based on the assessed state of the stock, and there are separate guidelines for each state ("decision rules", Punt & Hilborn 1997). In Finnish lakes, the density of vendace is a determining factor that influences the growth rate of whitefish, and this has to be taken into account in fisheries management. Specific decision rules are needed for the states of low and high vendace densities, coupled with rapid and slow growth rates of whitefish, respectively. Overdense, dwarfed whitefish stocks are special cases, where mass removal is the only effective measure to remedy the situation.

6.5. Management of mixed fishing of whitefish and brown trout

The results of decision analysis from Lake Lappajärvi (V) and Lake Päijänne (Heikinheimo & Valkeajärvi 1998) showed that it is possible to apply such fisheries management that stocking of both whitefish and brown trout in the same lake is profitable. However, if the target was to enhance the natural reproduction of brown trout, the minimum allowable mesh size in gill nets should be at least 60 mm (Auvinen et al. 1998). Managing the whitefish fishery would then be difficult. One compromise is to apply the mesh size restriction only in the pelagic area, although the young brown trout are then not perfectly secured. Other possible measures are to allow the fishing of small-sized whitefish only in the spawning areas during spawning time (II), to close the stocking areas of brown trout to fishing, or other case-specific local or seasonal restrictions. In practice, the management of a multispecies fishery in inland waters has often led to complicated regulations which consist of a combination of mesh size restrictions, gear-specific seasonal and areal restrictions, and closed seasons (Korhonen 2000).

Here, restrictions on trap net or trawl fishing were not considered, because these gear types are used by commercial fishermen only, and in most

cases vendace is the primary target species. Brown trout is caught occasionally but small individuals can be released and most of them survive (Turunen et al. 1994). Whitefish becomes important during the low-density periods of vendace. Moreover, restrictions on commercial fishing could have economic consequences, which should then be included in the analysis.

The benefits and risks of overfishing caused by the alternative mesh size restrictions in the gill-net fishery are considered in Table 5 (I, II, IV, V, Heikinheimo & Valkeajärvi 1998). To protect endangered predator fish stocks in whitefish lakes, there may be no other solution than to prohibit gill-net fishing in certain areas (Salmi et al. 2000). Similarly, areas where the tourist fishery in particular will be supported could be allocated to recreational fishing with rods only.

6.6. Indirect effects of whitefish fisheries management on the predation on vendace

On the basis of our findings (VI), the restriction of mesh sizes in gill-net fishing does not affect the predation by brown trout on vendace markedly, although the rod fishermen would benefit from the planned restriction (medium mesh sizes prohibited) by catching more large brown trout (Heikinheimo & Valkeajärvi 1998). Because the brown trout favour small prey fish (Niva 1999), most of the predation pressure is concentrated on the 0+ age group in early summer, when fishing has not yet greatly affected the abundance of newly released brown trout. During low vendace densities, large brown trout mainly consume other species, or adult vendace (Koivurinta et al. 2000).

The conclusion about the role of brown trout and perch as predators of vendace was that perch is more significant (VII). The main reason is that perch is more abundant and hence able to cause high predation pressure even if the predation was restricted to a short period. Another important feature is the assumed behaviour of perch, occupying the pelagic zone when the vendace stock is sparse (Helminen & Sarvala 1994, Valkeajärvi & Bagge 1995). This phenomenon causes depensatory mortality in the vendace at a range of vendace densities (VII), and the recovery of the

vendace from a low-density state may be prevented.

There is evidence of predation by perch on vendace in the pelagic zone from, for example, Lake Puruvesi (Jaatinen et al. 1999, Vuorimies & Tolonen 1999, Auvinen et al., unpublished). According to these findings, in Lake Puruvesi, even more young-of-the-year vendace were eaten by the perch population in the pelagic zone than by the salmonid predators. In Lake Päijänne, the situation in 1982 lends support to a similar hypothesis: a strong vendace year class was born during a high stocking density of brown trout, but a low density of perch (VI).

In the predator–prey systems (including fishermen–fish stock systems), a drop in the stock size of the prey below a threshold value may lead to the collapse of the stock (Holling 1973, Hilborn & Walters 1992). However, Myers et al. (1995) found poor evidence of such compensatory dynamics in fish stocks. This is in accordance with the results of the modelling approach on the effect of

predation on vendace (VII), where only the type II functional response caused a total collapse in the vendace stock. Although the available data indicates that the type II response would be possible in the brown trout–vendace interaction (VII), and in the predation by lake trout (*Salvelinus namaychus*) on its prey species (Eby et al. 1995), in reality a type III response with a low saturation level is more probable, which is in accordance with Hildén (1988). This conclusion is based on the fact that it is hardly profitable for the predator to hunt the prey at extremely low densities, and hence, a shift to other prey must occur. In such a case, predation could maintain the vendace stock at a low level, but would not cause extinction.

Smelt is another species that may play an important role in the dynamics of vendace, or plankton-feeding whitefish. This species is not well-examined, and exhibits large variation in abundance and growth (Belyanina 1969). Smelt may be a plankton-feeder or a predator, depending on the individual size, and is generally considered a

Table 5. Benefits and risks of overfishing or underexploitation in the different scenarios of the management of the gill-net fishery in lakes with coregonids and brown trout or other salmonids, assuming no change in fishing effort.

Management decision on gill net mesh size	Exploitation of small-sized whitefish	Growth overfishing of rapidly-growing whitefish	Recruitment overfishing of native <i>C. l. nilssonii</i> and <i>pallasii</i>	Result from brown trout stocking	Protection of endangered salmonids
No restriction	Effective	Yes	Yes	Poor	No
Minimum 45 mm, only gill net fishing	Moderate	Possible (during sparse vendace stock)	Possible	Moderate	No
Minimum 45 mm, trawls or trap nets are used	Effective	Possible (during sparse vendace stock)	Possible	Moderate	No
Minimum 55 mm, only gill-net fishing	Ineffective (dwarfing possible)	No	No	Good	Moderate
Minimum 55 mm, trawls or trap nets used	Moderate, not caught with gillnets	No	Not probable	Good	Moderate
Medium mesh sizes prohibited (36–54 mm)	Effective	Possible	Possible	Good	Moderate? (Areal restrictions necessary)

potential food competitor of vendace (Sterligova 1979, Sterligova et al. 1995). However, vendace and smelt are able to avoid competition by temporal, spatial and behavioural segregation (Karjalainen et al. 1997). Predation on young-of-the-year vendace by smelt is possible (Sterligova 1979), and might then be an important factor during low-density periods of vendace, similar to predation by perch. On the other hand, smelt young are important as an alternative prey for brown trout, especially when the size of young-of-the-year vendace exceeds the prey size optimum for the predators (Vehanen et al. 1998, Koivurinta et al. 2000).

6.7. Multispecies models in fisheries management research

The significance of the ecosystem effects of fisheries has been widely recognized (Gislason et al. 2000), and therefore, single-species approaches are in many cases considered insufficient in fisheries management research (Christensen 1996). More complex models would be required that take into account functional interrelationships among ecosystem components (Murawski 2000). There are technical interactions (by-catches) and biological interactions, such as density-dependence, competition and predation. In the whitefish fishery, the role of both types of interactions is obvious.

Multispecies models can improve our understanding in at least two ways: (1) through a more realistic treatment of uncertainty and variability in population parameters, such as natural mortality, and (2) by representing additional non-target species and ecological linkages among species, either of which could be altered through fishing (Hollowed et al. 2000).

The key question in the management of vendace fisheries is, what causes the sudden collapses or recoveries in vendace stocks, and how could these be controlled? A model based on the equilibrium assumption (VI) cannot answer these questions. The assumption is justified as long as the recruitment of vendace is moderately steady, such as during the low-density period from 1983 to 1996 in Lake Päijänne (VI). However, the complex interactions and feedback mechanisms presumed between perch and vendace (Valkeajärvi

& Bagge 1995) could not be incorporated into the equilibrium model (VI). The effect of a functional response was inaccurate in a rough model where average population sizes for each year quarter were used. The functional response is determined as the number of prey eaten by one predator as a function of prey density per small unit of time (Murdoch 1973). Dynamic modelling is an effective tool in studying the complex interacting mechanisms that regulate the density of vendace stocks, such as the stock-recruitment relationship, predation by different species, functional responses in predation, inter- and intraspecific competition, and fishing (VII).

In Finland, the use of multispecies models in fisheries research has been uncommon. The first attempt was a three-species system model for Lake Inari (Marttunen & Kylmälä 1997), which included whitefish, vendace and brown trout. An earlier version of the model was presented by Marttunen (1992). The model included the stock-recruitment relationship for whitefish and vendace, predation by brown trout, fishing, stocking of whitefish and brown trout, and other optional interactions. The model was calibrated to the data from Lake Inari, but contained several uncertain parameters and was laborious to use (Marttunen & Kylmälä 1997).

Complex food web models are hardly usable as tools for fisheries management (Hilborn & Walters 1992, Francis & Shotton 1997). The model should have a suitable level of complexity: it should be able to represent the managed system adequately, but on the other hand, models too complex are vulnerable to mis-specification and inadequate parametrization (Sainsbury et al. 2000). The most crucial interactions can be included in the model as accurately as they are known. Ignoring important factors leads more probably to erroneous conclusions and recommendations than incorporation of uncertain information into the model. Such issues can then be addressed through further experimental work and through the analysis of data gathered to reduce the uncertainties (Hildén 1997).

The dynamic model presented in article VII cannot be used to predict vendace densities in Lake Päijänne because of several uncertain parameter values. This generally concerns the use of multispecies models for long-term predictions (Hol-

lowed et al. 2000). However, the modelling approach brought new insight into the interaction between vendace and the main predator fish species. An important benefit from this approach was that the most crucial parameters affecting the conclusions were recognized: the S/R relationship and the form of the functional response curve. In this study (VII), the effect of fishing was not examined. It is reasonable to assume that the same parameters are important in assessing the effect of fishing, and more effort should be directed towards research on these issues. This concerns whitefish as well, because dome-shaped stock-recruitment relationships and wide variations in recruitment occur in whitefish, especially in pelagic stocks (Salojärvi 1992a).

6.8. Treating the uncertainty

The methods of decision analysis are well-suited to handling the problems in fisheries management, because contradictory objectives, and the demands of different types of fisheries can be taken into account. Secondly, uncertainty is an important element in fisheries management. Decisions have to be made, even if there were deficiencies in the basic information, or a large natural variation in the parameter values. Uncertainty is included in the basic information used in fish stock assessment, both in the state of the variables and in the causal relationships (Kuikka 1998). An assessment of risks connected to different management options should be a part of fisheries management research (Kesteven and Holt 1955, Precautionary approach... 1995, Francis & Shotton 1997).

The advantage of influence diagram models (V, VI) is the flexible handling of uncertainty. Influence diagrams can include both structural and parametric uncertainty, and other models, such as Y/R or cohort analysis models can be connected to the influence diagram models (Varis & Kuikka 1997). The starting point in decision analysis is that the value of information is determined according to its ability to change a decision. The variables that play a significant role in fisheries management can be identified and therefore require more detailed examination (Clemen 1996, Kuikka et al. 1999).

Uneven recruitment poses problems in the exploitation of vendace and pelagic whitefish. If the fluctuation of fish stocks is considered for the most part random, it is difficult or impossible to control by fisheries management. The hypothesis of multiple equilibrium states is a more plausible explanation for the behaviour of fish assemblages (Holling 1973, Hilborn & Walters 1992, Amundsen et al. 2000). The interactions between the species determine which kinds of stable states are possible, but random factors play a significant role in determining the state in which the stock ends up in each situation. A shift from one state to another requires a significant perturbation from the current state.

The concept of multiple equilibrium systems would make it understandable that for instance the dwarfing of whitefish may become a permanent situation, not easily affected with ordinary fisheries management measures. Different mechanisms are involved in maintaining the state of a dense stock. As an example, the parasites often become abundant in dwarfed whitefish stocks, which decreases the value of the catch and thus hinders the exploitation of the whitefish (Amundsen 1988). Short-term management in such a case does not lead to any improvement, because the state of the stock easily returns to the previous state (Amundsen et al. 2000). Only effective long-term fishing is able to produce a permanent amelioration. The same concerns the biomanipulation of eutrophicated lakes by the mass removal of fish, which aims at restructuring the biological community (Peltonen 1999).

The possible equilibrium states in complex fisheries systems can be examined only by dynamic modelling. In cases where several nonlinear mechanisms interact, an equilibrium assumption can yield misleading results (VI, VII). Even a model in which the main uncertainties are included may not be very useful for the needs of fisheries management without an understanding of the underlying dynamics (VI, VII). For instance, knowing that a vendace stock is expected to fluctuate over a wide range of densities does not help the fisheries manager, if he does not know which factors cause the fluctuation and how it can be manipulated.

Simple models are effective tools for studying such basic properties of a dynamic system as

stability and limit cycles, which are the basis for understanding ecological systems (DeAngelis 1988). In Finland, the use of dynamic models in studying fish stocks, such as the fluctuations of vendace stocks, has been minor, although there is plenty of data from different lakes.

A determining feature in adaptive fisheries management is learning from experience and modelling. Simulation of both the management decision and the ecological systems with models is an important tool in adaptive management (Sainsbury et al. 2000). Multispecies models can also be used as a basis for developing hypotheses, which could then be tested through adaptive management (Hollowed et al. 2000). The biological models should be expanded to include important social and economic effects (Stephenson & Lane 1995).

7. Conclusions

7.1. Main issues facing the management of the coregonid fishery

The major issues facing the management of the coregonid fishery are:

- The polymorphism of whitefish, which implies that sympatrically living whitefish may exhibit widely differing living habits and growth rates
- Interactions between whitefish and vendace
- The ecosystem effects of the fishery, such as by-catches and the effects of fishing and fisheries management on biological interactions in the ecosystem, which may have profound and unexpected influences
- Differing goals of fisheries management in different types of fishing: the commercial, subsistence and recreational fisheries, and other interests, such as protection of endangered fish stocks
- Uncertainty in the parameters of fish stock dynamics, mainly due to environmental effects and biological interactions such as predation and competition.

7.2. Present management situation

In the present management situation, the exten-

sive mandate of decision-making in Finland at the local level in the statutory fisheries associations and in the fishery regions has created in principle the potential for flexible management of the fisheries. The stocking obligations settled by the courts to compensate for habitat modifications were very rigid in the past, but currently, shifting to other species for stocking is possible if necessary, as is use of some of the resources for ameliorative measures other than stocking. Generally, many fishermen are aware of the necessity to manage fisheries to maintain a sustainable fishery, and they are willing to cooperate.

The main problems in the current coregonid fisheries are the following:

- Extensive fish stocking is carried out and the stocking density of whitefish is not always in balance with the fishing effort in the lake; moreover, the whitefish forms of stocks used are chosen more or less intuitively. Stocking is the most common compensatory measure settled by water courts, but often not profitable.
- There has been a lack of knowledge on issues of great significance to the management of coregonid fisheries, such as how to affect the fluctuations of vendace stocks, the suitability of different whitefish stocks for managing purposes, and, up to the early 1990s, the right stocking densities of whitefish.
- The coregonids respond sensitively to changes in the environment and in the fish assemblage, which increases the unpredictability of the development of the fishery system.

In addition, there are general problems in Finnish fisheries management that affect the coregonid fisheries as well:

- The goals and objectives of fisheries management are in many cases not explicitly determined.
- Different types of fishery are mostly present in the lakes to be managed, and contradictions cannot be avoided.
- The areal units for which fisheries management is planned are generally too small and do not cover whole lake systems; the restrictions on fishing are too complicated and incoherent within the lake system
- Although the monitoring of the fish stocks and

the fishery belongs to the duties of the statutory fishery associations or fishery regions, the resources are often a restricting factor, and the data gathered is insufficient for drawing conclusions about the state of the fish stocks.

7.3. Implications for practical management of the whitefish fishery

The determining factors to be considered in the management of coregonid fisheries are

— **The type of fishery: recreational, subsistence or commercial fishery**

Lakes with only one type of fishery, for instance pure recreational fishing areas, are exceptional in Finland. In most cases, all types are present, and there are conflicting management needs (Fig. 15). A common source of controversy is the gill-net fishing on whitefish which takes young salmonids as by-catch.

— **The whitefish forms present**

No general rules can be laid down for the management of whitefish, or a whitefish form. In Finnish lakes, there are different combinations of whitefish forms living sympatrically, and the stocks of the same form may differ in behaviour in different environments and fish assemblages. The division of whitefish into forms is obscure. Moreover, an introduced stock may exhibit a different life strategy and growth rate in the new environment. The most common case is the combination of a slowly-growing, pelagic stock and a rapidly-growing stock, which currently often originates from stocking. Even in cases of several sympatric whitefish stocks (e.g. Lake Inari), these two types are relevant. Declined, threatened whitefish stocks are a special problem in many lakes.

— **The presence of vendace**

Fluctuations in the vendace stock are a dominating factor in coregonid lakes, because the density of vendace greatly affects the commercial fishery and has profound influences in the fish assemblage, regulating for instance the growth rate of whitefish. As a preferred food for predators, vendace may also regulate the growth of salmonids.

— **The presence of endangered salmonid stocks**

The gill-net fishing of whitefish and protection of naturally reproducing salmonids in the same lake is a contradiction that is still unresolved.

A key question in avoiding contradictions between different interest groups in coregonid lakes is the goal-setting of the fisheries in each case. Is each kind of fishery equally important in the lake, or does some type dominate? Even if management decisions are mostly compromises, the high potential for a significant tourist fishery, for instance, emphasizes the recreational aspects of fisheries management (Fig. 15). The main features of management in different cases would be the following:

- 1) Recreational fishing as the dominant interest:
 - gill-net fishing strictly restricted (only large mesh sizes allowed), with the exception of vendace gill nets and perhaps the spawning time of lake-spawning whitefish.
- 2) Commercial and subsistence fishing dominant:
 - less strict restrictions on gill-net mesh sizes (e.g. medium and large mesh sizes allowed).
- 3) All types of fishing equally important:
 - a combination of different kinds of regulation: mesh size restrictions on gill nets (e.g. medium mesh sizes prohibited), possibly different rules for specific depth zones, case-specific areal or seasonal restrictions.
- 4) Lakes with endangered salmonid stocks
 - strict restrictions on gill-net fishing, closed areas and seasons.

In lakes where different types of fisheries are present, a suitable restriction on the mesh sizes used in gill nets (small or medium mesh sizes prohibited) can ensure a moderate yield from native whitefish stocks, and whitefish and brown trout stocking. Here, accurate mesh size limits are case-specific because of the varying growth rates of whitefish in different lakes, and dependent on whether or not there is commercial trawl or trap net fishing. Specific regulations for different depth zones may be effective, such as the prohibition of small and medium mesh sizes in the deep-water zone to protect young salmonids, but no restriction on shallow waters. To protect endangered fish stocks, strict restrictions on gill-net fishing, closed areas and seasons are all inevitable.

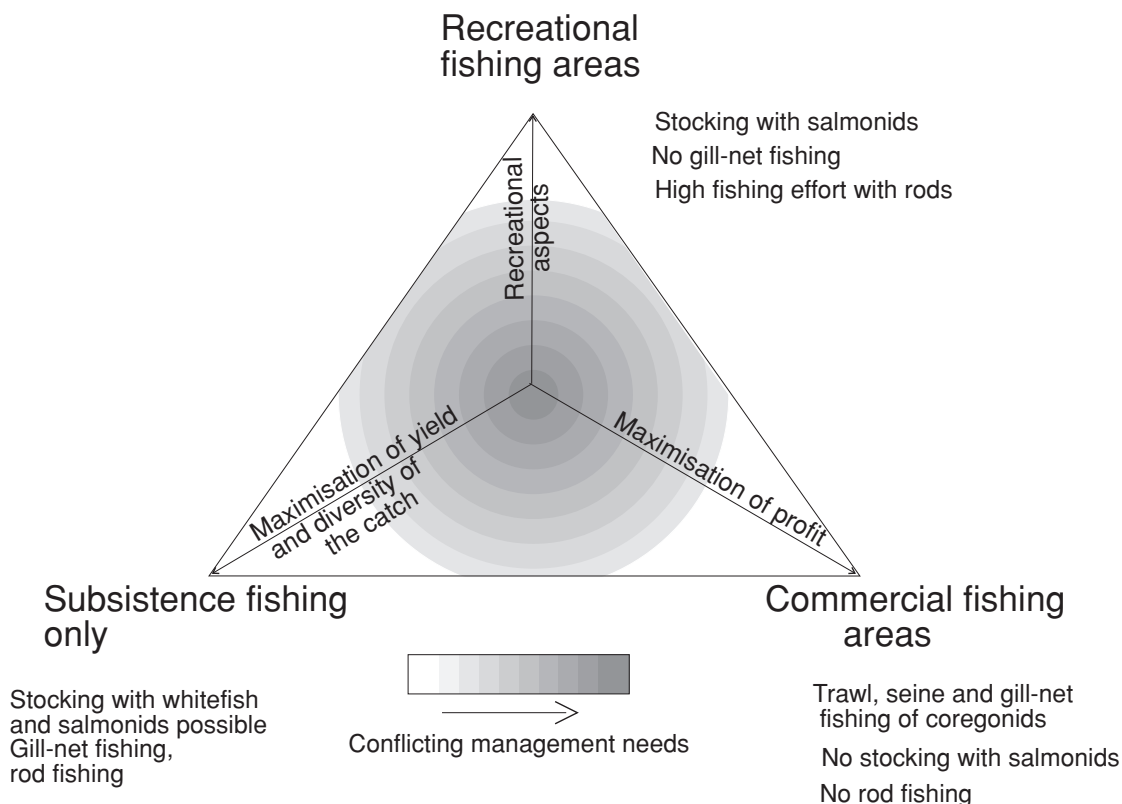


Fig. 15. A schematic presentation of the main interests and typical features of the three different types of fishing in Finnish coregonid lakes. Generally, different types of fishing are exercised in Finnish lakes simultaneously, and the pure fishing types are theoretical. The risk of conflict is largest in situations where all types of fishing are equally important.

Other important aspects in the management of coregonid fisheries include the following:

- **Fisheries management in coregonid lakes should be adaptive and flexible** enough to respond rapidly to new situations, and to apply suitable decision rules in each situation. In lakes with significant coregonid fishery, monitoring of the coregonid stocks is necessary to detect possible signs of coming changes. The key variables to be monitored are catches, growth, density (catch per unit of effort in numbers) and age distribution. Fishery regions should as far as possible co-operate in monitoring and management planning to create coherent fisheries management for more extensive entities within the lake systems.

At the end of the 1990s, a monitoring system

CORNET (Finnish Coregonid Stock Research and Monitoring Network) was started in the 14 most important vendace lakes in Finland, including Lakes Paasivesi and Päijänne, carried out in collaboration by the Universities of Joensuu, Jyväskylä and Turku, and the Finnish Game and Fisheries Research Institute, and financed by the fisheries administration, fishery regions and other organisations as well. This project will provide information for the local planning of fisheries management, and long-term data for research.

- **In vendace lakes, specific decision rules are needed for the different states of the coregonid fishery system:** the states of high and low vendace density, which are reflected in the growth rate of whitefish and salmonids, and accordingly, in the mesh size restrictions needed.

- **The necessity of whitefish stocking should be critically considered**, in particular in lakes with strong native whitefish or vendace stocks, and the stocking densities should be in balance with the fishing effort. Introducing whitefish stocks from distant areas should be avoided.

7.4. Implications for research

1) The adaptive management implies monitoring and modelling research

A determining feature in adaptive management is learning from experience and modelling. The decision rules for management are updated on the basis of gathering new data and knowledge (Fig. 16). Through modelling it is possible to examine the effects of different measures without having to put them into practice. In reality, because of the uncertainty caused by environmental disturbance, the impact of a given management measure may be impossible to detect in the short term by monitoring fish stocks.

2) Dynamic modelling is needed in the research on the effects of fishing and fisheries management on the complex interactions in fish assemblages

Simulating the ecological system with dynamic models is the only way to examine the simultaneous effects of complex non-linear interactions in fish assemblages. Equilibrium models can lead to biased conclusions and management advice for fish stocks that exhibit complex dynamics. The results of the dynamic modelling studies can be used as a basis for new hypotheses, and be incorporated into decision analysis models to assess the effect of uncertainties and to develop decision rules (Fig. 16).

3) Decision analysis is recommended for fisheries management research on coregonids

Incorporation of uncertainty into the models used for fisheries management research is essential. Sensitivity analysis is used to outline the effect of the uncertainties, especially whether the decisions were affected, and the

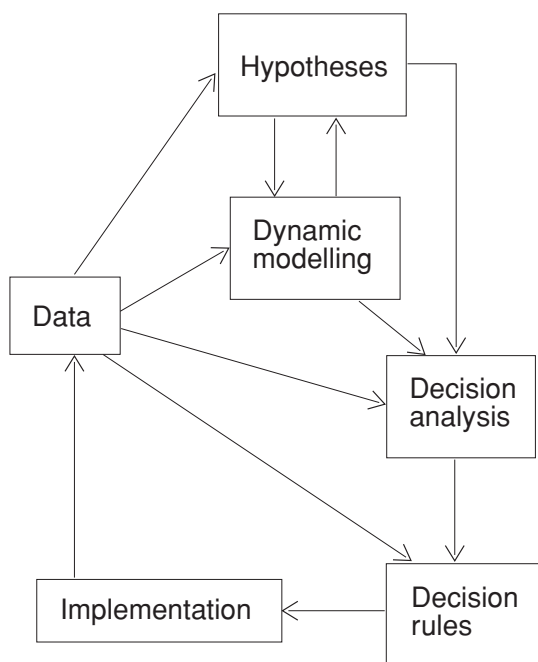


Fig. 16. Main links between adaptive fisheries management and modelling research. Data is used to update the hypotheses and models, and to choose the decision rules to be implemented.

benefits and risks in alternative management scenarios are assessed. The methods of decision analysis, such as Bayesian influence diagrams, have proved to be promising tools for handling the uncertainty in the coregonid fisheries, and for treating contradictions between different types of fisheries. The biological models should be expanded to include important social and economic effects.

4) Needs for future research

In the fisheries management of coregonids, a great deal of the uncertainty is caused by the variation in the natural mortality, interactions within the fish assemblage, and imperfect knowledge of these issues. To reduce the uncertainty, the biological issues and variables that need the most attention in future research are, (1) mortality in the non-recruited age groups (e.g. post-stocking mortality in whitefish); (2) stock-recruitment relationships in coregonids; and (3) effect of predation and fishing on the fluctuations of vendace stocks.

Here, the functional responses in the predation on vendace, and in fishing on vendace are crucial.

The flexible use of different kinds of models is highly recommendable to broaden the understanding of the dynamics of fish stocks and fishing, and to handle various cases. Because of the dominating role of vendace in the coregonid lakes, management should aim at moderating the fluctuations in the recruitment of vendace which would benefit both the vendace and whitefish fisheries.

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